Understanding predation risk in fisheries: Octopus depredation in the southern rock lobster (*Jasus edwardsii*) fishery in Australia

by

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STATEMENTS AND DECLARATIONS

Declaration of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University. All research conducted for this thesis was approved by the University of Tasmania Animal Ethics Committee (Permit No. A0010843).

Signed

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GENERAL ABSTRACT

Depredation within fisheries occurs when a predator preys upon target species caught within fishing gear. In many cases predators can be habituated to commercial catches from fisheries, especially when prey are too large or too fast for the predator to forage successfully in the natural system. Depredation in fisheries has received much attention over the last few decades in light of conservation and economic implications. Current knowledge is still focused, however, on the direct impacts of depredation on fisheries (e.g. financial losses), or predator populations, without consideration of the implications for prey populations.

Recent advances in predator–prey theory have demonstrated that predation not only generates direct impacts on prey populations via consumption, but also has indirect impacts via causing changes in prey activity, behaviour, physiology and development, i.e. 'non-consumptive' effects of predation or predation risk. For example, prey under predation risk are forced to make behavioural choices between vital activities, such as feeding and predator avoidance, by reducing activity or seeking out shelters. Hence, individual-level decision making (e.g. sheltering vs feeding) can have profound implications on prey life history traits such as survival, growth and reproduction, which can in turn impact populations and ecosystems. In regards to the prey, consumptive and non-consumptive effects have not yet been thoroughly examined in a fishing context, particularly on fishing grounds where predator habituation to fishing gear occurs and the implications may be extended to the prey population.

In this thesis, the interaction between the Maori octopus (*Pinnoctopus cordiformis*) and the southern rock lobster (*Jasus edwardsii*) is used as a predator–prey case study, with particular emphasis on octopus depredation within the southern rock lobster fishery (SRLF) in Australia. A multi-level approach examines predation risk at the population level from fishery-dependent

information on fishing grounds, and at the individual level from laboratory experiments designed to elucidate the physiological responses of lobsters under predation risk. In-pot lobster mortality is used as a proxy of predation risk for the fishery (i.e., 'in-pot predation risk'), and its examination across spatial and temporal scales and with a range of life history traits forms the basic understanding of this case study. At a finer-scale individual level, information from experiments provides new insights on prey decision-making processes under predation risk, elucidating the non-consumptive effects of octopus predation on lobster. Specifically, this study comprises four linked, but stand-alone, chapters addressing the following: understanding spatio-temporal patterns of octopus predation in the SRLF (Chapter 2) and the identification of lobster life history traits associated with octopus depredation in the SRLF (Chapter 3); and the examination of physiological responses of adult *J. edwardsii* under predation risk (Chapter 4); and how such responses can be altered under the combination of temperature and predation risk in key lobster life stages such as sub-adults (Chapter 5).

Different spatial and temporal patterns in octopus depredation were found in the SRLF, demonstrating the dynamic nature of this predator–fishery interaction. Using fisheries information from Tasmania, it was evident that while octopus depredation reached maximum levels during winter on the east coast, predation risk increased during summer time on the west coast. Such spatial-temporal variability in predation risk was examined further with time series modelling using fishing and environmental variables as explanatory variables of in-pot lobster mortality within stock assessment areas. Most eastern areas showed a stronger effect of fishing variables, such as lobster CPUE and fishing effort, than sea surface temperature, with the opposite pattern along the west coast. A classification of SRLF stock assessment areas based on predation risk levels was developed and implications for fisheries management highlighted.

In-pot predation risk increased with lobster size and was elevated for male lobsters (i.e., size- and sex-dependent mortality). The effect of individual traits of *J. edwardsii* such as body length and sex on in-pot predation risk was examined in the fishing zones of South Australia, using mixed-modelling techniques. Predation risk was also associated with the catch rate of lobsters (used as a proxy of lobster abundance), revealing a density-dependent rate of mortality that varied among fishing zones. Findings from these two components of the thesis provide new insights on spatial and seasonal

components of predation risk in the SRLF, how predation risk was related to lobster life history traits, and the ecological and economic implications associated with octopus depredation on the lobster fishing grounds.

Individual-level information from physiological experiments revealed that lobster metabolism was strongly affected under predation risk scenarios. Adult individuals exposed to predator cues (kairomones) during the nocturnal-active phase of lobster activity reduced their metabolism as a predator avoidance mechanism. Low metabolism is suggested to reflect lobster inactivity or sheltering. Although such an anti-predator response may serve as a strategic mechanism to survive, deleterious effects on other vital functions such as feeding are expected to influence rates of growth and reproduction and affect population-level dynamics.

In defining lobster decision making under predation risk (e.g. feeding vs. sheltering), environmental changes associated with temperature (e.g. warming waters) may force individuals to be more active during high-risk scenarios in order to satisfy metabolic demands. This was examined in sub-adults *J. edwardsii* using an experimental approach combining predation risk and thermal acclimation scenarios; the latter was used as a proxy of projected temperatures for the south-east Australian region under climate change. Individuals acclimated at warming temperatures (e.g 23°C) did not exhibit anti-predator responses such as a reduction of metabolic rates observed in sub-adults at ambient temperatures (20 °C). Instead, lobsters at warmer temperature increased their activity once energetic requirements were elevated. This suggests that anti-predator responses such as sheltering may be cancelled under projected temperatures for the region. Such findings can be used as a proxy to understand how climatic variability associated with climate change can generate direct impacts on the survival of individuals, and indicate the longer-term implications for local ecosystems and fisheries.

This study provides insights on depredation in fisheries by articulating information at different organizational levels. Hence, it provides an ecological framework to examine fishing grounds as high-risk environments for lobsters, serving as a baseline for future studies on predation risk and its implications for lobster populations. At the same time, findings from this thesis will provide a better understanding of predator–fishery interactions, which can enhance fishing management especially in the context of implementing ecosystem-based fishery management.

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Chapter 1:

General introduction and thesis structure

Understanding direct and indirect relationships between species within marine communities is a fundamental requirement for developing a comprehensive picture of community ecology (Ohgushi et al. 2012). One of the most ubiquitous and critical of all species interactions is predation, with direct effects on prey populations via density-mediated effects (predator responses, Holling 1959), as well as altering prey individual traits (i.e. trait-mediated or non-consumptive effects, Peacor and Werner 2001). Predation can trigger dramatic changes in ecosystem functioning through top-down trophic cascades (Frank et al. 2005), but also by the varied effects of predator avoidance (Long and Hay 2012). A holistic understanding of predator–prey interactions is fundamental to the implementation of ecosystem-based management (Pikitch et al. 2004; Tyrrell et al. 2011)

1.1 Predation in marine fisheries

Predation is considered as a pervasive yet ephemeral feature in fisheries (Bax 1998), and represents a large source of fish mortality, which in many cases exceeds the mortality rates imposed by commercial fisheries (Tyrrell et al. 2011). Most of our understanding of predation in fisheries is conceived in terms of functional and numeric responses of predators (Bax 1998; Hunsicker et al. 2011), although some studies have highlighted the significant impact that predators may have for the foraging and social behaviour of marine fishes (Bax 1998). Prey individuals under the risk of predation can strongly modify key traits such as behaviour, morphology, life history and physiology to maximize survival (Lima and Dill 1990; Werner and Peacor 2003; Hawlena and Schmitz 2010; Sheriff and Thaler 2014). Such trait-mediated effects of predation are also known as the non-consumptive effects (NCEs) of predation risk which can have severe, even fatal impacts on prey (Preisser et al. 2005), affecting prey demography (e.g. Zanette et al. 2014), community structure and ecosystem processes (Trussell et al. 2006; Schmitz et al. 2010). We have a poor understanding of the indirect effects of predation in the context of fishing, however, which highlights the need for an enhanced understanding of predator–prey interactions and their effects on fisheries in an ecosystem management context (Bax 1998; Tyrrell et al. 2011; Hunsicker et al. 2011). What is required is an

examination of predator–prey interactions from the individual- to the ecosystem-level, with a particular emphasis on the spatial and temporal scales at which fisheries operate and are managed (Hunsicker et al. 2011).

1.2 Depredation in marine fisheries

Predators can directly interact with fisheries, generating mortality by consuming organisms from the fishing gear during capture, known as 'depredation' (Uhlmann and Broadhurst 2013). Information about depredation in marine fisheries has been mostly reported from top predators such cetaceans (e.g. odontocethes, Hamer et al. 2012), sea birds (Tuck et al. 2011) and sharks (e.g. Barnett et al. 2010) interacting with long-line fisheries (reviewed by Silva et al. 2011; Hamer et al. 2012). Nevertheless, depredation can occur in a variety of fishery systems, including trap-based fisheries for lobsters and crabs where teleosts (e.g. conger eel, O'Sullivan et al. 2003), elasmobranchs (e.g. catsharks, Barnett et al. 2013) and cephalopods (e.g. octopus, Rodhouse and Nigmatullin 1996; Boyle 1997) are common mid-trophic predators within fishing gear. Compared with depredation by top predators, there is less known about depredation by mid-trophic predators despite the significant economic (e.g. Brock and Ward 2004) and ecological (e.g. Shester and Micheli 2011; Barnett et al. 2013) implications. Ecosystem impacts also exist as predators and fisheries compete for the same stock causing direct (e.g. through removal) or indirect (e.g. through trophic cascades) impacts on target fish stocks (Hamer et al. 2012).

1.3 Octopus depredation

Depredation by octopus has been the subject of research on crab and lobster fisheries from the beginning of last century (Garstang 1900) as octopus are common predators of lobsters and crabs caught by traps (reviewed by Boyle 1997). Most octopuses are generalist predators, displaying an opportunistic feeding behaviour that is linked to prey abundance and environmental conditions (Boyle

and Rodhouse 2005; Robin et al. 2014). Adult lobsters and crabs caught in traps are unable to escape from foraging octopuses, which can enter traps and remove prey before they are harvested by fishers. Depredation risk by octopus is difficult to predict given typically strong inter-annual variation, particularly within areas that experience extreme temperature variation (Garstang 1900; Rees and Lumby 1954), which demonstrates the strong environmental dependency of octopus foraging ecology (e.g. under ENSO, Cortez et al. 1995) and population dynamics (Rodhouse et al. 2014).

Crustacean fisheries can also be negatively impacted through the consumption of bait by octopus in lobster traps (Brock et al. 2003; Smith 2003; Groeneveld et al. 2006). Despite the economic impacts of lobster mortality and bait consumption, effects of octopus predation have been underestimated in many fisheries (Groeneveld et al. 2006), and poorly examined in most others (Groeneveld et al. 2006). Octopus depredation has been mostly examined in lobster fisheries of the genus *Jasus* occurring in the southern hemisphere, such as the southern rock lobster (*Jasus edwardsii*) fishery (SRLF) in Australia (Brock and Ward 2004; Hunter et al. 2005; Harrington et al. 2006) and New Zealand (Ritchie 1972), as well as in the *Palinurus gilchristi* fishery in South Africa (Groeneveld et al. 2006).

1.4 The octopus–lobster fishery interaction in south eastern Australia as a case study

The southern rock lobster is one of the most important fishery resources (commercial and recreational) in the states of South Australia, Victoria and Tasmania (Jeffs et al. 2013). Commercial fisheries in all three states are quota managed (Jeffs et al. 2013). The total annual catch is approximately 3,000 tonnes, estimated at around AU$200 million (ABARES 2012).

1.4.1 Consumptive effects of octopus depredation (inside the fishery)

In-pot lobster mortality within the southern rock lobster fishery (SRLF) is mostly due to predation by the Maori octopus (*Pinnoctopus cordiformis*), formerly known as *Octopus maorum*

(O'Shea 1999; Brock and Ward 2004; Harrington et al. 2006), which is the largest octopod in Australasia (Norman and Reid 2000). Octopus depredation can easily be identified and observed by fishers as lobsters are killed without damage to the exoskeleton, and appear to be 'sucked clean' (Boyle 1997). This distinctive predator 'fingerprint' has allowed this interaction to be reported in studies undertaken in Tasmania over the long term (Hunter et al. 2005; Harrington et al. 2006) and South Australia (Brock and Ward 2004).

Current understanding of octopus depredation in these fisheries is spatially and temporally restricted given the limited spatial scale and 10-year time gap since local studies were undertaken (Hunter et al. 2005; Harrington et al. 2006). Between 2000 and 2010, significant reductions in lobster catch rates have occurred due to large inter-annual variability in recruitment (Linnane et al. 2013). There is thus a need for a more recent and advanced analysis that can consider and integrate fishing, life history traits and environmental variables to characterize octopus depredation at a range of spatial and temporal scales.

Current understanding of density-dependent mechanisms operating in octopus depredation in the Tasmanian SRLF was reported by Hunter et al. (2005). Their study suggests that depensatory mortality occurs as an inverse relationship between lobster catch rates and lobster killed by octopus within pots. A characterization of density-dependent mortality is needed including key demographic traits such as size and sex as both can affect important fishing metrics (e.g. catchability) in the SLRF (Frusher and Hoening 2001; Ziegler et al. 2004). A better characterization of consumptive effects of octopus depredation can help define predation risk levels across the various habitats in which the lobster population occurs. Additionally, an up-to-date and detailed examination of the octopus–lobster fishery interaction is highly desirable given the strong environmental and ecosystem changes in regions where *J. edwardsii* fisheries occur, such as south-eastern Australia where there is ongoing evidence of climate change (Pecl et al. 2009, 2014).

1.4.2 Non-consumptive effects of octopus depredation (outside the fishery)

While octopus depredation can be directly quantified from lobster pots, the non-consumptive effects associated with the octopus–SRLF interaction are largely unknown and unexplored for lobster populations.

Predators such as octopus can strongly modify rock lobster habitat use and distribution as the lobsters act to reduce predation risk (Berger and Butler 2001; Butler and Lear 2009). Rock lobsters, as well as other crustaceans, are able to detect octopus presence by chemical cues (e.g. Ross and Boletzky 1979; Berger and Butler 2001; Sakamoto et al. 2006; Buscaino et al. 2011; Gristina et al. 2011). Octopus presence can trigger dramatic behavioural responses in crustaceans resulting, in most cases, in a reduction of activity or immobility of the crustaceans (see Hazlett 2011). However, it is not known how the presence of *P. cordiformis* may lead to changes in activity patterns of *J. edwardsii*, particularly during nocturnal periods when both octopus (Mills et al. 2008) and lobster (MacDiarmid et al. 1991) become more active. There may be dramatic implications of octopus depredation on the fishing grounds with uncertainties concerning lobster foraging ecology and migration, particularly in those areas where octopus depredation is elevated.

1.5 The south-eastern region of Australia – A risky environment for *J. edwardsii*?

The south-east Australian region is one the fastest warming regions in the southern hemisphere (Hobday and Pecl 2014). The intensification of the South Pacific Gyre has led to the southward penetration of the East Australian Current (EAC) (Ridgway 2007), a warm nutrient-poor current that is the main oceanographic driver for the region (Ridgway 2007). In Tasmania, warming temperatures and the extension of the EAC has facilitated the settlement of a habitat-modifying sea urchin (*Centrostephanus rodgersii*) which has resulted in the formation of urchin barrens, i.e. reef areas stripped of most macro algae (Ling et al. 2009).

Jasus edwardsii plays a key ecological role on Tasmanian rocky reefs as it helps control the numbers of urchins and hence the overgrazing as large lobsters are a key sea urchin predator.

Nevertheless, lobster capacity to control urchins has been decreasing as the abundance of lobsters has declined, including those of large lobsters (Ling et al. 2009). Importantly, the ecosystem service that lobsters provide to Tasmanian rocky reefs may also be affected by changes in octopus abundance and distribution as warmer waters may facilitate growth and reproduction of cephalopods (Robin et al. 2014).

Prey species adaptively allocate their foraging efforts and therefore their exposure to predation across high-risk and low-risk situations (the predation risk allocation hypothesis, Lima and Bednekoff 1999). Such foraging efforts, however, can be modulated by environmental stressors such as temperature (Killen et al. 2013; Culler et al. 2014; Matassa and Trussell 2014), as the energetic demands and foraging rates in ectotherms are regulated by the physiological effects of temperature (Angilletta et al. 2003; Dell et al. 2014). Hence, anti-predator mechanisms such as sheltering can be altered under warming-water scenarios, as increasing foraging rates are expected to compensate for elevated energetic maintenance demands. Rapid changes in water temperature may alter anti-predator behaviors, such as sheltering in *J. edwardsii*. Such alteration are likely to be elevated for small individuals as sheltering behaviour is strongly correlated with lobster size (smaller individuals remain in shelters for greater periods of time than larger individuals, e.g. Wahle 1992). It is unknown how sub-adults lobster ecology and physiology may respond under the elevated temperatures in combination with predation risk. This is particularly relevant in the context of reducing the current uncertainties of the ecological and economic role of *J. edwardsii* under projected climatic variability in the south-east Australian region (Pecl et al. 2009, 2014).

1.6 Stress physiology under predation risk – from individuals to ecosystems

Predation risk reduces prey foraging rates or increases the use of refuge habitats by prey (Sih 1985), negatively affecting prey growth and fitness (Trussell et al. 2006; Slos and Stoks 2008). This implies profound alterations to prey physiology associated with the re-allocation of resources away from growth and reproduction behaviour and processes designed to maximize survival (Hawlena and

Schmitz 2010). The redirection of energy and nutrients of prey can change important ecosystem functions such as nutrient cycling and the efficiency of energy transfer across trophic levels (Trussell et al. 2006; Schmitz et al. 2010). Hence, the physiological stress response of prey to predation risk has been recently suggested to represent a common and fundamental mechanism that is independent of the taxon, and of space and time. This mechanism can help to explain context dependency in prey demography (Zanette et al. 2014) and ecosystem functioning (Hawlena and Schmitz 2010), with recent applications to marine ecosystems (Trussell et al. 2006; Matassa and Trussell 2014).

As an important component of stress physiology, respiratory physiology (e.g. oxygen consumption or metabolic rates) is a powerful approach to examine the impact of stressful conditions such as predation risk on aquatic organisms (Holopainen et al. 1997; Cooke et al. 2003; Steiner and Van Buskirk 2009; Gravel et al. 2011; Toscano and Monaco 2015). Energetic costs of predator–prey interactions can be quantified via measurement of metabolic rates (Cooke et al. 2003; Killen et al. 2013), providing robust information that can be integrated with fishery management and conservation (i.e., 'conservation physiology'; Cooke et al. 2013, 2014).Overall, the lack of mechanistic information regarding consumptive and non-consumptive effects of predation risk by octopus in fishing grounds limits the understanding of ecosystem and economic implications for lobster population and associated fisheries such as the SRLF in southern-eastern Australia. In defining such effects, a multi-level approach (from individuals to population) is an important requirement for developing a broader understanding of predator–prey interactions in marine fisheries (Hunsicker et al. 2011; Tyrrell et al. 2011).

1.7 Thesis aims and structure

In this thesis, the interaction between *P. cordiformis* and *J. edwardsii* is used as a case study of depredation in marine fisheries. The primary objective was to develop a multi-level approach to examine consumptive and non-consumptive effects of octopus depredation on the lobster population, with particular emphasis on the fishing grounds. This thesis reveals new insights on predator–fishery

interactions, providing a strong ecological framework for future studies on predation risk and its implications for lobster population and associated fisheries.

The thesis is composed of six chapters (Figure 1.1):

Chapter 1 – General introduction. This chapter provides a general overview on depredation in marine fisheries, with special emphasis on the octopus–SRLF interaction in Australia. Major gaps in knowledge are provided, as well as the approaches required to address the lack of such information.

Chapter 2 – This chapter examines key environmental and fishing factors that define spatio-temporal components of octopus depredation in the SRLF in Tasmania based on fishery-dependent time series data (2000–2011). Using time series analysis such as dynamic regression models, the lag effect of environmental (e.g. sea surface temperature) and fishing (e.g. lobster catches and fishing effort) factors provides key demographic information on predation risk levels across Tasmania.

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Chapter 3 – In this chapter a closer examination of the octopus–lobster interaction is conducted, including key life history traits such as size, sex, and lobster catch rate from a fishery-dependent time series (1993–2012) from South Australia. Using mixed modelling techniques, it was demonstrated that octopus depredation involved lobster size, sex and density on the fishing grounds.

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Chapter 4 – This chapter investigates the non-consumptive effects of octopus predation on lobster respiratory physiology. Oxygen consumption (metabolic rate) was used as a proxy of lobster activity under the exposure of octopus olfactory cues to simulate predation risk scenarios during night and day. This study demonstrates that *J. edwardsii* is able to detect *P. cordiformis* presence by chemical cues, mainly during night time. Additionally, threatened lobsters strongly reduced their

metabolic rates, suggesting a change in lobster activity (e.g. immobility) under octopus presence. Findings from this study are discussed in relation to other anti-predator mechanisms, providing new insights on physiological responses under predation risk in lobsters and marine invertebrates.

Chapter 5 – This study provides key mechanistic information concerning the energetic costs of *J. edwardsii* sub-adults under predation risk and elevated temperatures. Here, lobsters were acclimated under thermal scenarios simulating projected temperatures for the south-eastern region in Australia under climate change (Pecl et al. 2009). Using different metabolic parameters, I defined the future energetic costs of *J. edwardsii* under predicted ocean warming, demonstrating that temperature can offset anti-predator responses in this species, complicating the response of lobster populations and associated fisheries in the future.

Chapter 6 – This is a general discussion that synthesizes major findings from all data chapters (chapters 2 to 5). Here, I discuss how consumptive and non-consumptive effects of octopus depredation can impact lobster populations and associated fisheries in south east Australia. Additionally, this chapter explores how such effects could be integrated into current fishery management, contributing to the operationalization and implementation of ecosystem-based management.

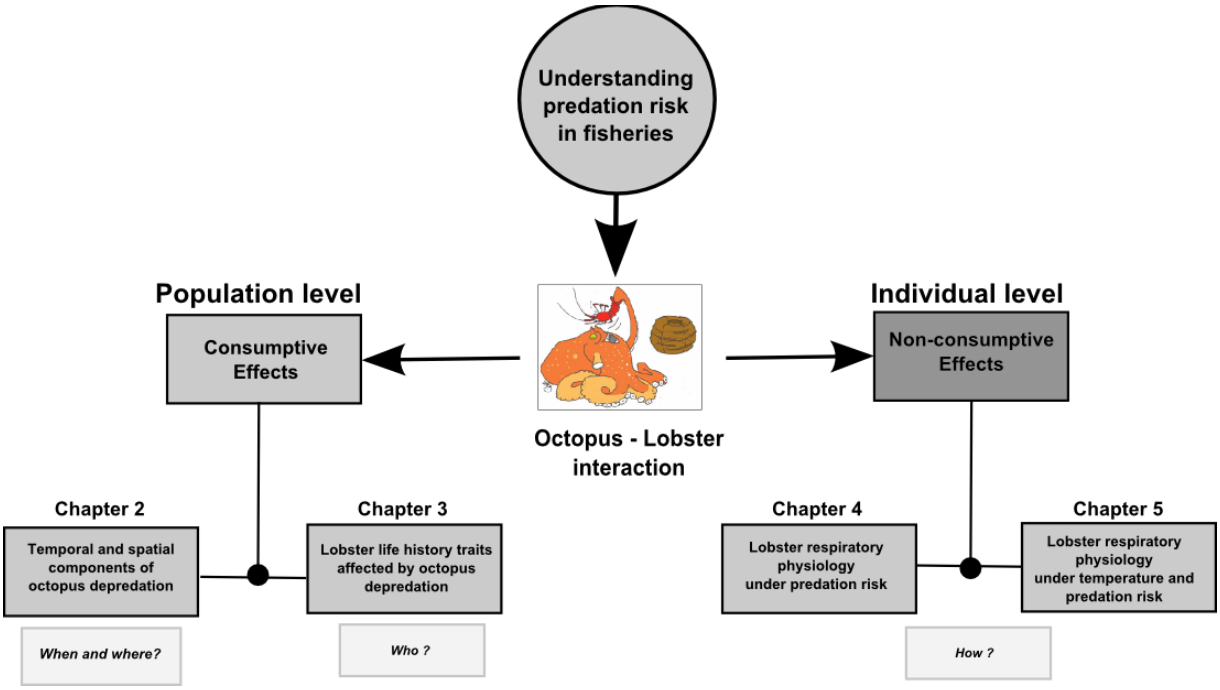

Figure 1.1: General diagram of the components of this thesis.

1.8 References

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Chapter 2:

Spatial variation in mortality by octopus depredation in the Tasmanian rock lobster fishery

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Preface:

This work has been published in a refereed journal and is presented below in identical form, excepting minor suggestions/additions from thesis referees. The citation for the original publication is:

Briceño F, León R, Gardner C, Hobday AJ, André J, Frusher SD, Pecl GT (2015) Spatial variation in mortality by in-pot predation in the Tasmanian rock lobster fishery. Fisheries Oceanography, doi:10.1111/fog.12115.

2.1 Abstract

Capture of target species using pots or traps can be affected by interactions that occur inside fishing gear. For example, some predators are able to directly kill or damage commercial catches from fishing gear, which is identified as mortality by depredation. In the Tasmanian southern rock lobster fishery (SRLF), depredation by octopus is known to vary spatially, assumed to be in response to different environmental and ecological conditions. However, these effects are not well understood and there is concern that changes in the system as a result of climate change may alter the spatial distribution and extent of octopus depredation. Using fishery-dependent commercial time series data (2000–2011), we first examined how in-pot lobster mortality by octopus varied across fishing areas at inter- and intra-annual scales. These spatial and temporal patterns were examined using dynamic regression models (DRM) using lagged variables of lobster abundance (lobster catch per unit effort CPUE), fishing effort (pot lifts) and environmental variables (sea surface temperature, SST). This demonstrated that lobster mortality by octopus depredation in most areas was strongly affected by the current lobster CPUE (indicating an instantaneous direct impact), whereas fishing effort and SST differed spatially in terms of lag selection and correlation sign. Most eastern Tasmanian areas showed a stronger effect of fishing effort rather than SST, with the opposite pattern along the west coast. We provide the first classification of SRLF stock assessment areas based on predation risk level and identify the explanatory fishing and environmental factors.

2.2 Key words

Lobster mortality; octopus depredation; Tasmania; time series analysis; dynamic regression models

2.3 Introduction

Trophic interactions (e.g. predator/prey relationships) in marine fisheries have received much attention over the last few decades associated with the implementation of ecosystem-based management (EBM) (Botsford et al. 1997; Pikitch et al. 2004). To achieve the goals of EBM, biological as well as physical factors that influence productivity need to be integrated into the assessment of fisheries (Botsford et al. 1997; Jennings 2004). Trophic linkages are particularly important in understanding productivity, and can involve direct linkages (e.g. predator kills a prey) or indirect linkages (e.g. predation on shared prey resources) (reviewed by Bax 1998). Despite the potential for change in mortality via predation over time and its implications for productivity, mortality is usually considered a constant in stock assessments, which potentially introduces bias and reduces accuracy (Hollowed et al. 2000; Overholtz et al. 2008; Tyrrell et al. 2011). The risk of bias from assumed constant mortality is especially apparent where there are long-term environmental changes such as those associated with climate change where trophic webs are being altered by the redistribution of marine species (Cheung et al. 2010).

The response of species to climate change is likely linked to their interactions with other species, including through competition and predation. Changes in predator–prey interactions as a function of ocean warming are already resulting in challenges for biological and human systems, particularly in regions experiencing significant warming such as in south-east Australia (Hobday and Pecl 2014). Warming in this region is largely a function of the intensification of the East Australian Current, a warm nutrient-poor current flowing poleward along the eastern seaboard (Ridgway 2007a). Ecosystem responses include changes in macroalgae, invertebrate and fish assemblages on eastern Tasmanian rocky reefs (Ling et al. 2009; Johnson et al. 2011; Last et al. 2011; Stuart-Smith et al. 2013).

The southern rock lobster, *Jasus edwardsii*, is the second-most important commercial fishery resource in Tasmania in terms of gross value of product, and has been used as a case study of how Australian fisheries may be impacted by climate change (Pecl et al. 2009; Frusher et al. 2014). The southern rock lobster fishery (SRLF) experiences different fishing and environmental conditions

across Tasmania (Hartmann et al. 2012) (Figure 2.1). Higher lobster catches and catch rates occur in deeper waters on the western coast compared to the eastern coast; northern areas are characterized by warmer waters, which results in differences in maturity and growth (i.e. northern populations tend to growth faster reaching maturity at larger sizes) (Gardner et al. 2006). Lobster populations across Tasmania are expected to be affected by environmental as well as ecosystem changes, particularly along the east coast (Pecl et al. 2009; Johnson et al. 2011). For example, interactions between predators and prey can be modified due to differential responses to environmental changes (Abrahams et al. 2007; Domenici et al. 2007; Grigaltchik et al. 2012).

Lobster mortality would be affected by abundance of key predators such as octopuses which are highly responsive to environmental factors, especially temperature (Semmens et al. 2004). In Tasmania, the octopus - rock lobster interaction includes predation of lobsters that have entered pots and are thus less able to escape (Harrington et al. 2006). Such within-gear mortality by predators has been recently referred to as 'depredation' (Uhlmann et al. 2013). 'In-pot' lobster mortality and 'octopus depredation' are used as synonymous throughout this study. Lobsters that have been killed or damaged by octopus in pots result in considerable financial losses for the fishery (Brock and Ward 2004; Groeneveld et al. 2006). A small amount of octopus bycatch in the SRLF can be retained and sold, which results in compensatory income but considerably less than the loss of lobsters (Brock and Ward 2004) because the price per kg of octopus is only around 5% of that received for lobster.

The perception of rock lobster fishers is that more octopuses are being caught in lobster pots over time, which may be driven by an increase in octopus numbers as a consequence of recent ocean warming (Nursey-Bray et al. 2012). In-pot lobster mortality by octopus is estimated to represent 2.35% of the lobster harvest per year in the Tasmanian SRLF stock assessment (Hartmann et al. 2012), and is currently accounted for in the stock assessment via this single estimated value. Using a state-wide estimate of in-pot predation lobster mortality may bias assessments as fishing and environmental factors vary across the Tasmanian SRLF; hence, spatially resolved characterization of lobster mortality by octopus depredation could improve models used to guide management of this fishery (Gardner et al. 2015).

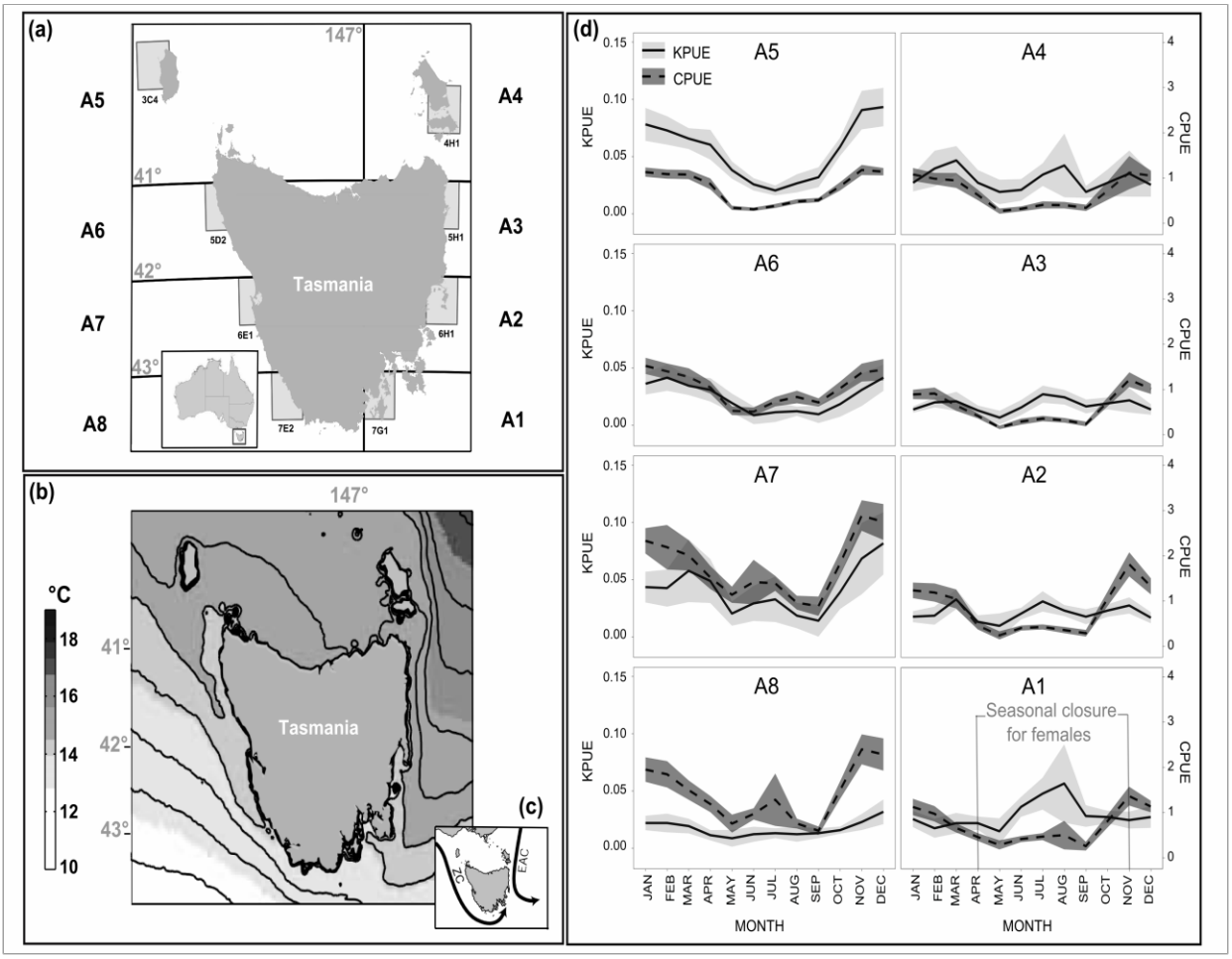

Figure 2.1: (a) Map of inshore stock assessment areas (A) of the Tasmanian Southern rock lobster (*Jasus edwardsii*) fishery, and selected fishing blocks (approximately 17.5 km x 17.5 km) used for this study. (b) Map with mean SST (1993–2004) (contour interval is 0.5) (extracted from Ridgway (2007b). (c) Main ocean currents in Tasmania: East Australian Current (EAC) and Zeehan current (ZC) (after Ridgway, 2007b). (d) Monthly distribution of killed lobster per unit effort (KPUE) (solid line) and lobster catch per unit effort (CPUE) (dashed line) across stock assessment areas. Monthly values were averaged between 2000 and 2011 with related confident intervals (mean + 1.96*standard error). The seasonal closure for females for all areas is indicated (April - November). Monthly distribution of fishing effort is provided as supporting information (Figure S2.1).

We first examined how predation of lobsters in pots by octopus varied across fishing areas at inter- and intra-annual scales using fishery-dependent time series data. Second, we explored the dynamic effect of fishing and environmental factors including lobster catch per unit effort, fishing effort and sea surface temperature using dynamic regression models (DRMs). We examined spatial variation in octopus depredation between 2000 and 2011 across stock assessment areas, and how monthly distribution of in-pot predation intensity also differs between the east and west coasts of Tasmania. Based on DRM outcomes, we present key fishing and environmental regressors to examine direction (positive/negative) and length (short/long) of effect for modelling in-pot lobster mortality by

octopus. We produced a classification of the Tasmanian stock assessment areas based on predation risk level and associated drivers for the fishery.

2.4 Methods

2.4.1 Octopus depredation observations from lobster fishers

The lobster–octopus interaction examined here is a species-specific interaction between *Jasus edwardsii* and the Maori octopus (*Pinnoctopus cordiformis*, synonym *Octopus maorum)* within commercial lobster pots. Lobsters killed by octopuses in pots can be easily identified by fishers as octopuses are the only predator able to extract lobster flesh without damaging the lobster's exoskeleton. This 'predation fingerprint' has allowed the mandatory reporting of lobsters killed by octopus depredation since 1993 in the Tasmanian commercial fisher logbook. Observations are collected daily during the fishing season in spatially referenced fishing blocks. Data used for this analysis was restricted to the period from 2000 to 2011 due to differences in logbook reporting and management prior to this period.

2.4.2 Time series data preparation

Daily observations included the number of lobsters killed by octopus, the number of live lobsters retained, and the median number of pots deployed each month over the period January 2000 to December 2011. Briefly, a lobster can be retained if it has legal size, if it's in season (as females have shorter seasons than males), not berried (as females can be legal sized and in-season but still berried), and if it's an acceptable product (e.g. lobsters that are damaged or too large are discarded). Time series were generated for specific fishing blocks representing all inshore stock assessment areas (Figure 2.1a), with fishing blocks selected by latitude in order to explore differences in environmental conditions among areas. Brock and Ward (2004) found that in-pot octopus predation in South Australia was higher in shallower waters than deeper waters. Given in-pot lobster mortality by octopus in the Tasmanian fishery occurs mainly in shallow waters, we constrained our dataset to shallow depths (0–20 m), which allows a more robust comparison among SRLF areas. The time series of lobsters killed by octopus and the number of live lobsters retained were standardized by total pot number and depth (≤ 20 m) to generate killed per unit effort ('KPUE') and live retained lobster catch

per unit effort (CPUE); the latter being a well-known proxy of abundance in fisheries (Maunder and Punt 2004).

Since the lobster pot acts as an encounter unit for the rock lobster–octopus interaction in lobster fishing grounds, we explored the effect of potting by adding the total fishing effort calculated as the median number of pots lifted by month ('POT') for each fishing block. The median of sea surface temperature ('SST') and maximum sea surface temperature ('MAX') by month were used as environmental proxies, with the latter used to explore extreme values (e.g. extreme warm events). We carried out a Box-Cox transformation to stabilize the variance of the data. Additionally, to better allow for across region comparisons, each time series was standardized separately by subtracting the mean and dividing by the standard deviation (Zuur et al. 2003).

2.4.3 Inter- and intra-annual trends in lobster mortality by in-pot predation

In order to understand how areas may differ temporally and spatially in lobster mortality via octopus depredation, we performed explorative plots based on the annual trends with associated intervals of confidence (IC = mean $\pm$ 1.96* standard error). Complementary information about the seasonal pattern of KPUE and lobster CPUE is also provided by normalized anomaly plots. In addition, intra-annual trends were examined using the 'predation proportion' which was calculated as the ratio between monthly KPUE and monthly total catch.

2.4.4 Dynamic regression models

We evaluated the dynamic effect of explanatory variables by dynamic regression models (DRMs). This linear modelling technique allows the explanation of the interactions and co-movements among a group of time series variables, and is used to specifically capture dynamic effects among regressors (Pankratz 1991). Lobster mortality by octopus depredation (KPUE) was modelled using lagged time series of KPUE (hereafter called 'endogenous regressors') and lagged time series of

fishing (lobster CPUE and POT) and environmental (SST or MAX) ('exogenous regressors') specified as follows:

where is the autoregressive coefficient for KPUE at different lags (*j*) (endogenous regressors), is the regression coefficient for the explanatory variables (exogenous regressors) and is the error term, which is assumed to be normally distributed.

DRMs are based on stationary multivariate time series, which implies no systematic changes in mean and variance (Box and Jenkins 1976). Thus, to obtain a DRM for each stock assessment area (regional DRM), we first decomposed each time series to remove inter- and intra-annual cycles using locally weighted regressions (Loess, R Development Core Team 2013). Once multivariate time series were de-trended and de-seasonalized, stationarity was tested by the Augmented Dickey-Fuller Unit Root Test and the Kwiatkowski-Phillips-Schmidt-Shin test (Zivot and Wang 2006). Endogenous (KPUE) and exogenous (CPUE, POT, SST or MAX) regressors were generated by lagging these variables by 12 months. Selection of regressors was performed by sequential replacement based on Schwartz's information criterion (BIC) from a maximum size of subsets equal to eight (package 'leaps', R Development Core Team 2013). This means that DRMs were based on a maximum number of eight parameters which reduced the risk of over-parameterization. The same procedure was performed by including only SST or MAX as regressors in order to avoid multicollinearity between these variables. SST and MAX models were compared by BIC, the model with the lowest BIC being selected. Selected regressors were then fitted by ordinary least squares (OLS) by minimizing the sum of square residuals. Afterward, multicollinearity was checked by variance inflation factor (Belsley et al. 1980).

Selected regressors were also assessed in terms of relative importance by decomposition of the coefficient of determination (R^2) by unweighted averages using the package 'realimpo' from Grömping (2006) implemented in R. Decomposition of R^2 is expressed as relative importance (%) by

normalizing all regressors to sum to 100%. Finally, goodness of fit was evaluated by residual standard error and multiple R^2, as well as model checking by visual exploration of model residuals.

2.5 Results

2.5.1 Inter- and intra-annual trends in lobster mortality by octopus depredation

Killed per unit effort (KPUE) and lobster CPUE differed among areas between 2000 and 2011, ranging between 0.061 kills/pot and 0.025 kills/pot in Area 5 (A5) and Area 8 (A8), respectively. Total kills across the whole period were estimated by multiplying regional KPUE by the total number of pots deployed across the years, producing the following order in scale between areas: A5 (1,076 kills) > A8 (527) > A7 (509) > A6 (425) > A1 (367) > A4 (355) > A2 (340) and A3 (255). Values of KPUE tended to vary more in in northern and western areas A4, A5 and A7 (Figure 2.2). Furthermore, octopus depredation in most eastern areas showed a clear decline. Although in-pot predation in northern areas (A4 and A5) was variable through time this temporal variation was not apparent in lobster CPUE, which remained stable. The opposite pattern was found in areas such as A8 where KPUE remained stable while lobster CPUE had large temporal variability. Additionally, anomaly plots (Figure S2.2, supporting information) show KPUE in northern areas (e.g. A5 and A6) followed a relatively similar seasonal pattern to lobster CPUE, although this pattern was not apparent in southern areas (A7 and A8).

The proportion of the catch killed by octopus depredation (predation proportion) differed substantially between the east and west coasts (Figure 2.3), with higher predation proportion in the east during winter (June -September) than summer (January–March). The proportion of predation that occurred in summer was relatively similar among eastern areas (mean $\pm$ SD = 2.5% $\pm$ 0.38%). Maximum peaks were evident in September in A1 (11.1%) and A2 (7.4%), and in June in A3 (8.4%) and A4 (9.15%). Western areas had less variation in predation proportion across months (around 2.5%) with the exception of A5 which ranged from 6% in September to 10% in June. A higher winter predation proportion in eastern areas was related to higher intensity of KPUE at low CPUE (Figure 2.1d). In addition, fishing effort in eastern areas was higher in winter than in summer (supporting information, Figure S2.1). In western areas, the seasonal pattern of catch and KPUE resulted in stability in predation proportion in most areas with exception of A5. Lobster CPUE was lower in the

northwest (A5) relative to other west coast areas and KPUE across months in A5 was higher than other west coast areas.

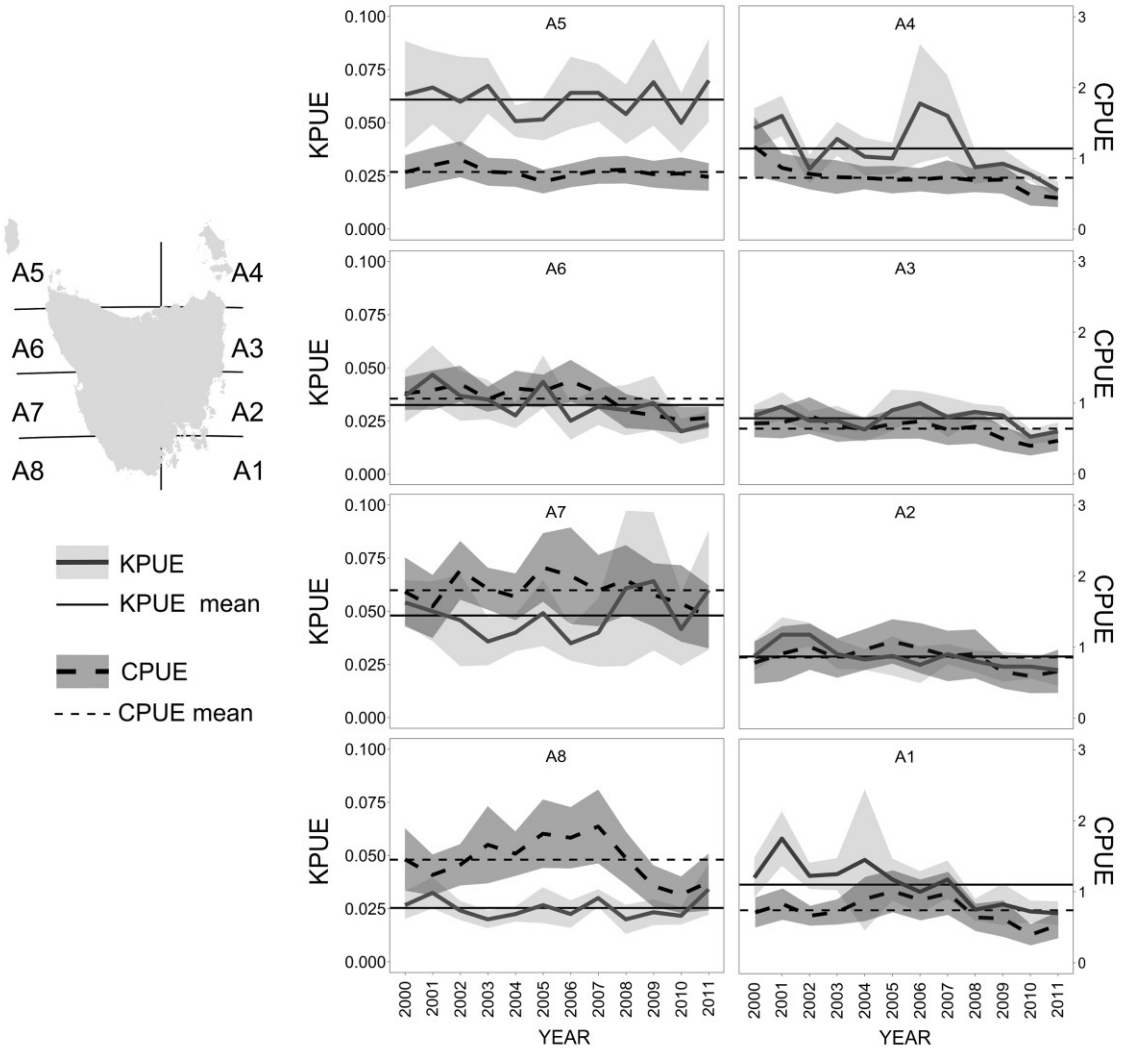

Figure 2.2: Inter-annual trends of killed lobster catch per unit effort (KPUE) (solid line) by octopus depredation and lobster catch per unit effort (CPUE) (dashed line) for each Tasmanian stock assessment area (A1–A8) between 2000 and 2011. Annual values were calculated by averaging months (January–December) with the confidence intervals (mean $\pm$ 1.96* standard error) expressing the intra-annual variability. Horizontal lines represent mean values of KPUE (solid) and CPUE (dashed) between 2000 and 2011.

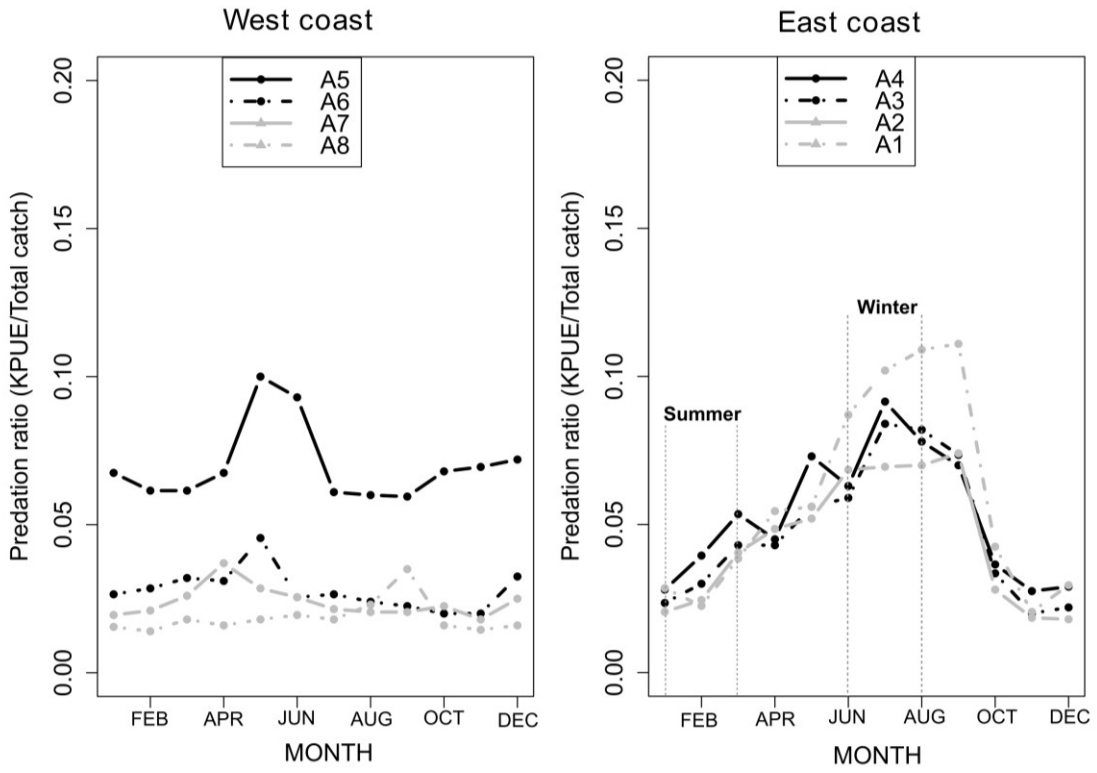

Figure 2.3: Monthly distribution of predation ratio (KPUE/Total catch) across Tasmanian stock assessment areas. Monthly median values were calculated between January 2000 and December 2011. Austral summer (January–March) and winter (June–August) are also specified.

2.5.2 Dynamic regression models

Regional models were composed of different numbers of endogenous and exogenous regressors (fishing and environmental variables) (Table 2.1). In terms of model accuracy, regional models related with the southern areas (A1, A7 and A8) had lower residual standard errors (RSE) than others areas. DRMs were relatively well fitted, with R^2 ranging between 0.51 (A5) and 0.71 (A7). Endogenous regressors were very similar among areas in terms of correlation coefficient and sign, with a consistent maximum coefficient at lag 2 and decreasing at longer lags (> 2 months). KPUE from two months prior (KPUE t-2) had an inverse correlation with present KPUE (t) (e.g. high/low KPUE today is related to a decrement/increment of KPUE two months ago). In addition, KPUE t-2 was a strong contributor to the R^2 in all areas (Figure 2.4), ranging from 25% (A1) to 48.1% (A4), showing the dependency of current lobster mortality on this regressor.

In terms of exogenous regressors, in most regional DRMs, lobster mortality was positively correlated with lobster CPUE with no lag (CPUE t). Lobster mortality was not correlated with CPUE in A4 and A7 at any lag. In addition, CPUE t contributed between 14% (DRM-A1) and 37% (DRM-A5) to model variance, showing the importance of this regressor in explaining lobster mortality. Fishing effort (POT) was also specifically selected in models for areas A1, A2, A4 and A5 at different lags and with different correlation signs. Most fishing effort regressors were of short lag (< 4 months), with a variance contribution ranging from 2.1% (A4, lag 4) to 14.3% (A1, no lag).

Mean and maximum sea surface temperature (SST and MAX respectively) were selected for a single east coast area (A2; MAX), and for most western areas (A6 SST) and (MAX; A7 and A8). In A2, a positive correlation between KPUE t and MAX t-4 was found. The same relationship was evident in A7 on the west coast, showing similar outcomes at the same latitude (Figure 2.1a). Here, an increment of KPUE t resulted from an increment of MAX four months earlier showing how MAX effects can persist over a relatively short time. In A6, KPUE t was directly affected by SST at lag 2, although at lag 6 and lag 7 a negative correlation was found. Indeed, SST at lag 6 in this particular area was the highest contribution (9.3%) of this proxy among regional DRMs. In addition, KPUE t in the DRM for A8 was inversely correlated with MAX at lag 10 and 11, showing a longer temporal effect of this variable in this area. In terms of variance contribution, SST and MAX had lower explanatory contributions (< 5%) compared to fishing factors, with the exception of SST t-6 in the DRM for A6 (9.3%).

Table 2.1: Dynamic regression models (DRMs) using fishing and environmental variables to model lobster mortality via octopus depredation across Tasmanian rock lobster stock assessment areas (A1–A8). DRM coefficients are specified by the following explanatory variables: killed lobster per unit effort (KPUE), lobster catch per unit effort (CPUE), total monthly effort (POT), sea surface temperature (SST) and maximum sea surface temperature (MAX). Length of lagging is specified by t-n, where n is the lag selected (in months) and no lag as t. Residual Standard Errors (RSE), multiple R2, and F ratio (degree of freedom) are showed. All selected regressors were significant at $p < 0.05$).

DRM	Endogenous regressors	Exogenous regressors	RSE	Multiple R^2	F (df)
DRM-A1					
	- 0.727 KPUE t-1	0.002 CPUE t	0.003	0.682	33.02 (123)
	- 0.941 KPUE t-2	0.002 POT t			
	- 0.701 KPUE t-3	0.002 POT t-2			
	- 0.494 KPUE t-4				
	- 0.282 KPUE t-5				
DRM-A2					
	- 0.993 KPUE t-1	0.404 CPUE t	0.413	0.712	37.99 (123)
	- 1.184 KPUE t-2	-0.144 POT t-11			
	- 0.988 KPUE t-3	0.448 MAX t-4			
	- 0.697 KPUE t-4				
	- 0.331 KPUE t-5				
DRM-A3					
	- 0.807 KPUE t-1	0.393 CPUE t	0.368	0.703	36.42 (123)
	- 1.246 KPUE t-2				
	- 1.180 KPUE t-3				
	- 1.133 KPUE t-4				
	- 0.780 KPUE t-5				
	- 0.467 KPUE t-6				
	- 0.284 KPUE t-7				
DRM-A4					
	- 0.815 KPUE t-1	0.212 POT t-1	0.399	0.641	31.65 (124)
	- 0.918 KPUE t-2	-0.203 POT t-4			
	- 0.636 KPUE t-3				
	- 0.424 KPUE t-4				
	- 0.154 KPUE t-10				
DRM-A5					
	-0.384 KPUE t-1	0.490 CPUE t	0.464	0.513	33.47 (127)
	-0.521 KPUE t-2				
	-0.286 KPUE t-3				
DRM-A6					
	-0.799 KPUE t-1	0.337 CPUE t	0.289	0.674	31.76 (123)
	-0.861 KPUE t-2	0.315 SST t-2			
	-0.565 KPUE t-3	- 0.549 SST t-6			
	-0.258 KPUE t-4	- 0.579 SST t-7			
DRM-A7					
	-1.124 KPUE t-1	1.430 MAX_{t-4}	0.005	0.715	38.51 (123)
	-1.565 KPUE t-2				
	-1.530 KPUE t-3				
	-1.124 KPUE t-4				
	-0.769 KPUE t-5				
	-0.350 KPUE t-6				
	1.713 KPUE t-9				
DRM-A8					
	-0.907 KPUE t-1	- 0.012 $CPUE_{t-4}$	0.002	0.594	22.46 (123)
	-1.042 KPUE t-2	- 0.830 MAX_{t-10}			
	-0.808 KPUE t-3	- 0.606 MAX_{t-11}			
	-0.587 KPUE t-4				
	-0.336 KPUE t-5				

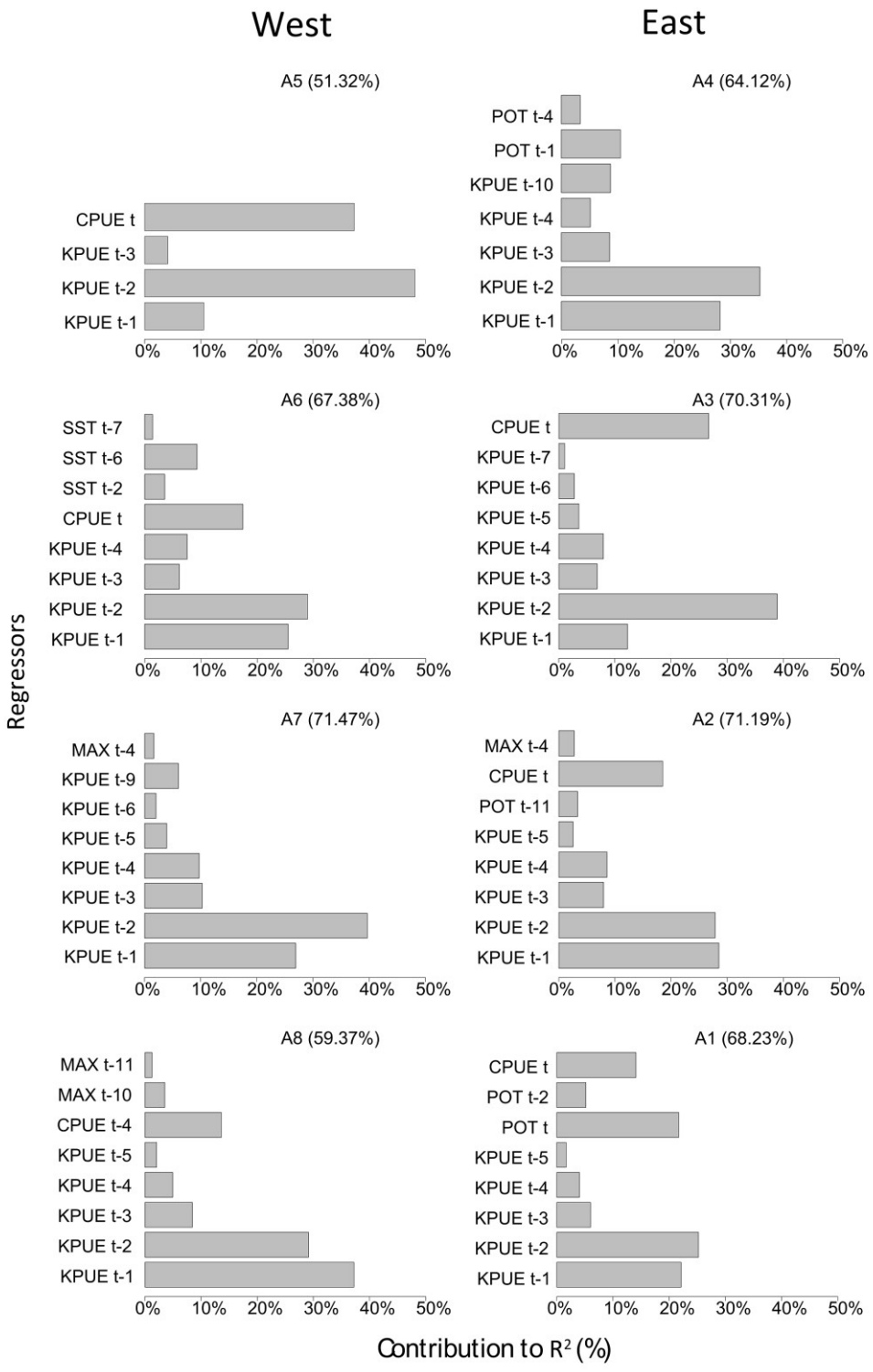

Figure 2.4: Variance composition of DRM regressors expressed as variance contribution by decomposing multiple R^2. Variables are specified as killed per unit effort (KPUE); lobster catch per unit effort (CPUE); fishing effort (POT); sea surface temperature (SST) and maximum sea surface temperature (MAX) by lagging. Number of lags are specified as *t-n*, where *n* is number of months prior. Present time or no lag is represented as *t*. Multiple R^2 is specified for each region as a percentage, hence regressors were normalized to sum to 100%.

2.6 Discussion

Generating accurate natural mortality estimates for fished species has received greater attention over the last few decades, both for improving single-species based management and for moving more towards ecosystem-based management (Jennings 2004; Pikitch et al. 2004). This approach benefits from empirical analysis of patterns in predation because values historically incorporated into stock assessments are often inaccurate and can bias conclusions (Hollowed et al. 2000). In the present study we demonstrated that lobster mortality by predation in pots varies considerably across stock assessment areas, and can follow seasonal cycles of fishing effort and lobster abundance. Such differences were also captured by DRM, generating further information about temporal relationships of fishing and environmental variables in relation to lobster mortality by predation.

2.6.1 Inter-annual variability in lobster mortality by in-pot predation

The Tasmanian SRLF experienced different levels of lobster mortality within pots between areas. Between 2000 and 2006, all eastern areas experienced an increase in KPUE through time, whereas from 2006 onward this pattern reversed, most strongly in southern areas (A1 and A2). In-pot predation in some of the western areas (A5 and A7) was variable between years with 'hot-spot' areas emerging in some years in terms of predation risk for the fishery. Additionally, negative anomalies of KPUE tended to be less frequent on the north-east coast (A3 and A4). Seasonal patterns in KPUE followed seasonal trends in CPUE, especially in the western areas and at King Island (A5).

High temporal variability in KPUE across years showed the unpredictable nature of octopus predation as reported in other shellfish fisheries (Garstang 1900; Cortez et al. 1995; Boyle 1997). The temporal decline in octopus predation after 2006 may be associated with the declining lobster abundance and CPUE experienced after 2006 across all areas (Hartmann et al. 2012). Hence, changes in lobster abundance may result in changes in octopus predation in the Tasmanian SRLF. This is consistent with observations in the South Australian fishery where high correlation between lobster

CPUE, octopus CPUE and KPUE (Brock and Ward 2004) implied that regional and temporal patterns in octopus predation were simply driven by differences in octopus population size.

Recent studies have demonstrated that the population genetic structure of *P. cordiformis* is highly variable across Tasmania and likely influenced by regional oceanographic drivers such as the East Australian Current (EAC) and the Leeuwin and Zeehan currents (Doubleday et al. 2009). Unfortunately, there is not information on demographic structure and population dynamics of this predator in Tasmania, which demonstrates the need for further studies. In addition, natural lobster mortality by octopus was reported from field studies in sub-adults suggesting that *P. cordiformis* is an important nocturnal predator on rocky reefs (Mills et al. 2008). Hence, future investigations should examine octopus dietary content to better understand this predator-prey interaction outside of the fishing gear.

2.6.2 Monthly distribution of predation proportion

Predation proportion differed markedly between the east and west coast Tasmanian stock assessment areas. In eastern areas the predation proportion was higher in winter than in summer. Once fishing and environmental factors are included, higher winter predation risk appears to be related to higher KPUE with low, but stable, CPUE during colder months on the east coast. Predation risk steadily increases towards winter in eastern areas when the SRLF deploys more pots. In contrast, predation risk in the western areas is stable throughout the year, although it varies spatially.

Despite all western areas showing a clear seasonal pattern in CPUE and KPUE, predation risk in the northwest (A5) was higher than in other areas, especially towards the austral autumn (fall). Higher predation at lower prey abundance (also defined as 'depensatory mortality') can result as a consequence of predator saturation according to the type II functional response defined by Holling (1959). In this context, Hunter et al. (2005) proposed that caught lobsters may be better able to avoid octopus predation when catch rates in pots are higher. The high winter predation reported in our study for some areas of the fishery is consistent with such a mechanism (Hunter et al. 2005), although the

fact that the pattern was not seen in many other areas casts some doubt on this as a generally applicable hypothesis.

The foraging behaviour of octopus may also be modified by temporal and spatial changes in fishing effort, resulting in changes in within-pot encounter rates between predator and prey. The Tasmanian southern rock lobster fishery increases its effort between May and July, especially in eastern regions (e.g. A1) where the winter-effort peak can be even higher than the summer one (Hartmann et al. 2012). A higher effort in winter may modify the encounter rate between octopuses and lobster caught as suggested in similar studies (Groeneveld et al. 2006).

Another possible explanation relates to fishery operations, with a female-harvest-closure season through winter and spring (April–November). As a result, lobster CPUE changes seasonally due to the female-harvest closure, but the number of killed lobsters reported is not split by sex and thus KPUE changes in relation to lobster CPUE may simply be because of the management of female landings. A similar result was expected to occur in the west coast, but this was not the case, at least for north-west areas. More studies are needed to resolve the influence of other fishing variables (e.g. soak time of pots) that may differ between east and west coasts, and that can seasonally vary due to changing sea conditions (e.g. winter) as reported in other lobster fisheries (e.g. *Homarus americanus*, Robichaud and Campbell 1991).

2.6.3 Lagging effect of fishing and environmental variables

The composition of regional models varied between fishing areas, reflecting differences in the effect of explanatory variables. Most regional models found a positive immediate effect of lobster CPUE on KPUE with no lag. This means that in most regions higher mortality occurred in pots when the catch rate of lobster in pots was higher. The consistency of this relationship may demonstrate a density-dependent predatory capacity of octopus such as broadly described in predator–prey relationships. Here changes in lobster catch rates may impact immediately on predation by octopus.

Fishing effort was the main factor affecting predation of lobsters in pots along the east and north-west coasts (A1, A4 and A5), with more fishing effort appearing to lead to higher mortality by octopus in these areas. The inclusion of effort as an explanatory variable allows a more complete explanation of how the predator interacts with the fishery. Even though both KPUE and lobster CPUE were standardized by pot numbers (< 20 m), potting itself generates an accumulative effect on fishing grounds, attracting both lobsters and predators through the bait used within the pots. Recent studies have shown the effect of bait as a food subsidy in lobster (*Panulirus cygnus*) fishing areas in Western Australia (Waddington and Meeuwig 2009), with potential ecological implications for lobster predators such as octopus (Phillips et al. 2012). A combination of bait and lobster can constitute up to 80% of the diet of octopus caught by lobster traps (South Africa, Smith et al. 2006). Although this pattern has not been quantified in Tasmania, observations within lobster pots by video cameras have shown that octopus can enter pots and may consume only the bait (Green 2002). Additional research is required to determine if this behaviour could reduce predation, or if shorter soak times would reduce predation as octopus first consumed bait.

In the west coast areas (A6, A7 and A8), the effect of environmental factors on KPUE was more consistent whereas on the east coast environmental factors only had a clear effect in A2. The east and west coasts differ in oceanographic conditions, with the east coast influenced by the East Australian Current (EAC), and the west coast influenced by the Zeehan Current (ZC) (Figure 2.1c). The ZC is strongest over winter and moves warm water down the west coast and southern tip of Tasmania, while the EAC is stronger over summer (Ridgway 2007b). Both SST and MAX affected KPUE in areas A6 to A8, which may be related to seasonal changes in the ZC. Long lags for MAX (10 and 11 months) were found exclusively in A8, which may be related to the inter-annual variability experienced by this region, resulting in negative correlations with lobster mortality. In addition, lobster mortality was explained by the same lag of maximum SST (lag 4) at the same latitude on both coasts (A2 and A7).

Even though the temperature has been reported broadly as a key environmental factor for cephalopod biology and ecology (e.g. Boyle and Rodhouse 2005), its effect differs along cephalopod life stages (Robin et al. 2014). Planktonic and juvenile phases of octopus are more vulnerable to

environmental changes compared with sub-adult and adult phases (Robin et al. 2014). This means that spatial and temporal patterns in KPUE due to difference in octopus abundance may be caused by environmental conditions in early development. Short lags show temperature also affects sub-adults and adults and thus their predation. This may be through processes such as changes in metabolic rate, but the mechanism is not clear from information available to this study. Climate change and variability experienced along the east coast of Tasmania could impact octopus predation through effects on different stages of life history, but further study is required to elucidate any patterns.

Outcomes of the DRM enabled the seasonal predation risk of SRLF areas to be categorised based on fishing and environmental variables (Figure 2.5). The east coast of Tasmania is a 'high-winter predation risk' zone for the fishery, where lobster CPUE and the amount of potting effort affects predation risk. In this region, predation risk increases with lower lobster catch rates and higher fishing effort during winter. The time response of lobster mortality to these fishing factors is either instantaneous or with only a short lag so any change in lobster CPUE and fishing effort would alter the predation risk quickly. On the west coast, in-pot predation is influenced by seasonal patterns in lobster CPUE and temperature. Predation risk was high in the northwest (A5), especially in autumn although had overall low predation risk in other western areas (A6, A7 and A8).

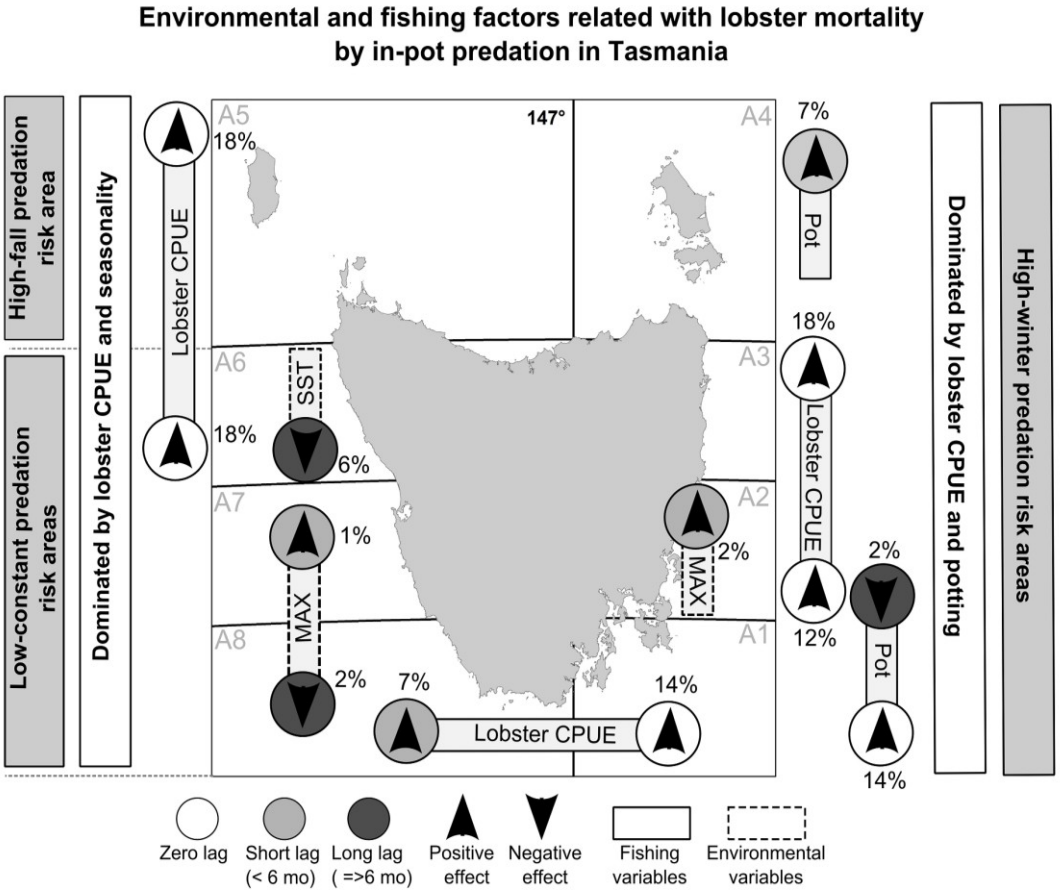

Figure 2.5: Map of Tasmanian rock lobster (*Jasus edwardsii*) fishery stock assessment areas indicating environmental and fishing factors related to lobster mortality by in-pot predation by octopus (*Pinnoctopus cordiformis*). Lobster per unit effort (lobster CPUE), fishing effort (POT), sea surface temperature (SST) and maximum surface temperature (MAX) are specified by correlation sign (positive, negative) and lagging (zero lag, short lag and long lag). Variance contribution of each regressor is specified and corrected by DRM multiple R^2. Eastern areas are classified as 'high-winter predation risk', and are mostly dominated by lobster CPUE and potting at no and short lag. Here, low lobster catches in cold months would be more susceptible to predation by increases in winter potting. On the west coast, two different areas are proposed: 'high-autumn predation risk', specific to A5, and 'low-constant predation risk' related to areas 6, 7 and 8. In-pot predation in all these areas follows the same seasonal pattern as lobster CPUE which informs how changes in lobster catches and seasonal temperatures may impact lobster mortality. In A5, the predation risk is higher than others especially in the austral autumn at low CPUE.

In Tasmania, in-pot lobster mortality results in a time and space averaged loss of 2.35% of the number of lobster caught. This figure is modest in terms of total removals, but could affect outcomes of decision-making, given that management adjustments to catch have been approximately 5% in recent years (Gardner et al., 2011). Currently the fishery management involves shifting of effort and catch spatially and temporally. Understanding patterns in octopus depredation could be included as additional mortality risks which may modify decision making for specific areas during closed seasons

while market price remains high. For instance, as only males can be landed in northern areas it is unclear how octopus depredation risk could increase to females leading to uncertainties at the population level. Likewise, outcomes from this study could better define sources of mortality in the eastern areas where there is a separate regional catch cap due to high accessibility to fishing, hence such areas tend to receive higher fishing mortality. This regional catch cap affects the time of effort on the east coast directly, but also leads indirectly to shifts in catch to other regions.

Stock rebuilding is being pursued in this fishery for economic objectives with fisheries managers setting lower catches to achieve higher catch rates (Gardner et al., 2015). The relationship between fishing effort, lobster catch rate and in-pot predation reported here shows that stock rebuilding would also benefit the fishery by simultaneously identifying lobster mortality sources as previously discussed. The understandings generated in the current chapter enables impacts on depredation to be better considered.

Biased stock projection from inaccurate or changes in predation estimates have been identified as an issue for other fisheries (e.g. Alaskan walleye pollock, Hollowed et al. 2000). This study showed that in-pot lobster mortalities were highly variable and with important differences between regions that could affect predation if spatial distribution of the catch and fleet changes. The effect of temperature was significant but small in magnitude, which implies that recent pulses in octopus depredation were not related to ocean warming, despite fisher concerns that this may have been the case (Pecl et al. 2009; Nursey-Bray et al. 2012).

This study represents one of the first attempts to characterize spatial and temporal components of mortality via depredation for a highly valuable fishery, *J. edwardsii* fishery in Tasmania. Whilst fishery-dependent data was suitable to examine dynamic aspects of fishing and environmental factors involved in octopus depredation, there are questions regarding octopus population dynamics and their impacts on lobster populations inhabiting fishing grounds that deserve further attention for future investigations. To achieve a complete understanding of octopus depredation, information on octopus-lobster interaction outside traps is pivotal. Integrating ecological information on predator and prey population dynamics would result in a stronger ecological framework for this case study, and thus

more accurate estimations of octopus depredation would be available to this fishery to enhance current and future management, particularly in the context of longer-term environmental change.

2.7 Acknowledgements

This study contributed to the project 'Preparing fisheries for climate change: identifying adaptation options for four key fisheries in south eastern Australia '(DCC & FRDC - Marine Biodiversity and Fisheries Climate Change, Project 2011/039). FB acknowledges Ph.D. scholarship support provided by the Chilean Government ('Becas Chile'), as well as financial support from IMAS. We appreciate suggestions and comments provided by Eriko Hoshino, Jayson Semmens and Eric Oliver (all IMAS) and Elsa Gärtner (IMAS) for generating the map in Figure 2.1, and editing plots.

2.8 Supporting Information

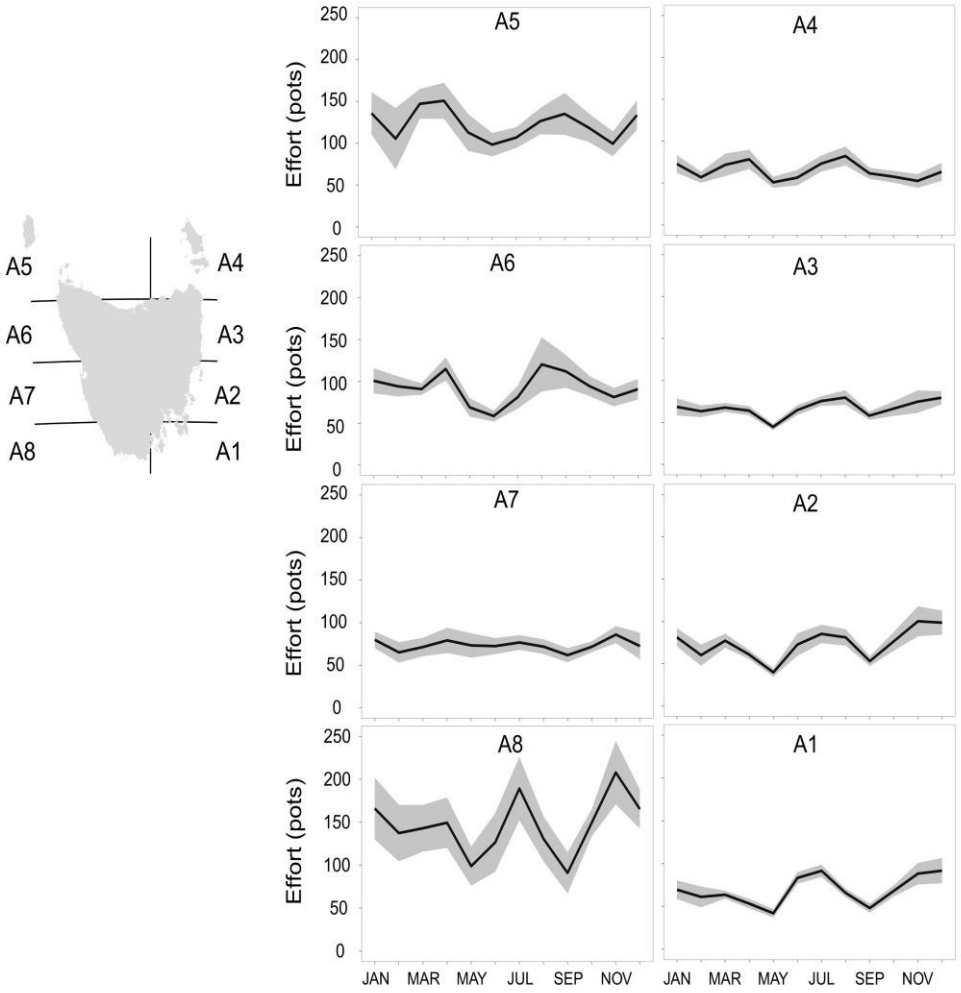

Figure S2.1: Monthly distribution of total effort (pots) in each of eight Tasmanian rock lobster (*Jasus edwardsii*) fishing areas (A1 – A8). Monthly values were calculated by median all year between 2000 and 2011. Intra-annual variability is expressed with the confidence intervals (grey bands) (mean $\pm$ 1.96*error standard).

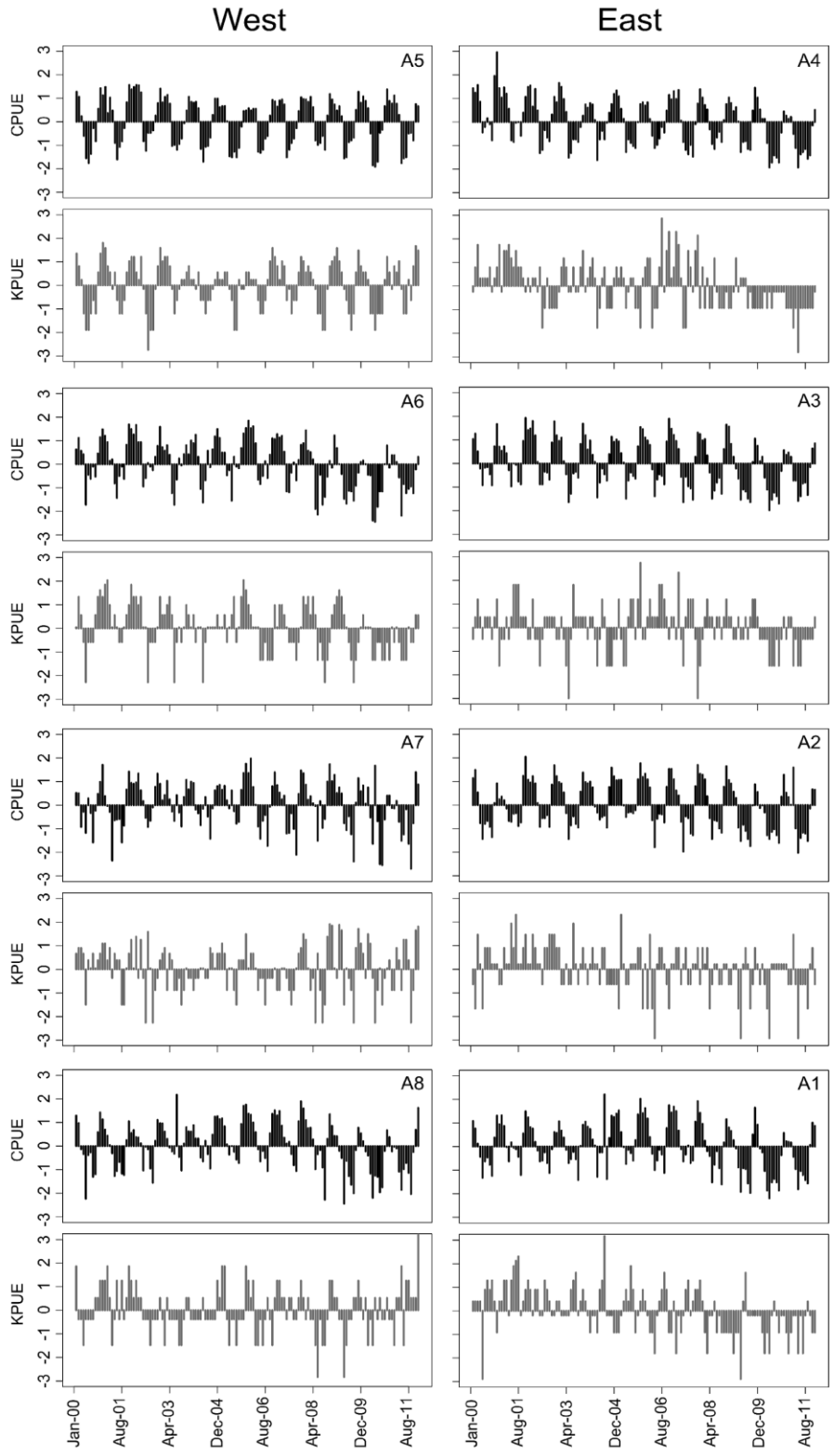

Figure S2.2: Normalized anomalies of lobster catch per unit effort (CPUE) (black bars) and killed lobster catch per unit effort (KPUE) (grey bars) time series from Jan 2000 to Dec 2011 for areas of the southern rock lobster (*Jasus edwardsii*) fishery in Tasmania.

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Chapter 3:

Lobster demographic traits associated with octopus depredation in the Southern rock lobster fishery in South Australia

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Preface:

This work has been published in a refereed journal and is presented below in identical form, excepting minor suggestions/additions from thesis referees. The citation for the original publication is:

Briceño F, Linnane AJ, Gardner G, Quiroz JC, Pecl GT (2015) Predation risk within fishing gear and its implications for Australian southern rock lobster fisheries. PLoS ONE 10(10):e0139816. doi:10.1371/journal.pone.0139816

3.1 Abstract

Depredation of southern rock lobster (*Jasus edwardsii*) within fishing gear by the Maori octopus (*Pinnoctopus cordiformis*) has economic and ecological impacts on valuable fisheries in South Australia. In addition, depredation rates can be highly variable resulting in uncertainties for the fishery. We examined how in-pot lobster predation was influenced by factors such as lobster size and sex, season, fishing zone, and catch rate. Using mixed modelling techniques, we found that in-pot predation risk increased with lobster size and was higher for male lobsters. In addition, the effect of catch rate of lobsters on predation risk by octopus differed among fishing zones. There was both a seasonal and a spatial component to octopus predation, with an increased risk within discrete fishing grounds in South Australia at certain times of the year. Information about predation within lobster gear can assist fishery management decision-making, potentially leading to significant reduction in economic losses to the fishery. For example, outcomes from this study can be of relevance to fishery management by defining areas times and areas where octopus depredation is elevated, which may be of use in defining temporal and spatial closures, as well as by including in-pot lobster mortality rates in annual biomass estimations.

3.2 Key words

Depredation; southern rock lobster; *Jasus edwardsii*; *Pinnoctopus cordiformis*; demographic traits; density-dependence; GLMM

3.3 Introduction

Predation plays an integral role in marine ecosystems influencing the structure and dynamics of ecological communities, with direct effects on prey populations via density-dependent mechanisms (e.g. predator responses, Holling 1959; Hunsicker et al. 2011), as well as indirect effects through altering prey behaviour and physiology (Trussell et al. 2006). In fisheries, predation is considered as a pervasive but ephemeral feature (Bax 1998) and represents a large source of fish mortality, which in many cases, exceeds fishing mortality (Tyrrell et al. 2011). Additionally, predators are able to interact directly with fisheries by preying upon target species caught within fishing gear, mortality known as 'depredation' (Uhlmann and Broadhurst 2013). Information about predator–fishery interactions have been mostly reported from top predator depredation in long-line fisheries (Hamer et al. 2012; Peterson et al. 2014; Tixier et al. 2014). However, depredation can occur in a variety of fishery systems, including trap-based fisheries for lobster and crab where teleosts (e.g. conger eels, O'Sullivan et al. 2003), elasmobranchs (e.g. catsharks, Barnett et al. 2013), and cephalopods (e.g. octopus, Boyle 1997; Brock and Ward 2004) are common mid-trophic predators within fishing gear. In contrast to depredation from top predators, the knowledge about mid-trophic predators interacting with crustacean fisheries has received less attention, despite substantial economic (Brock and Ward 2004) and ecological implications (Barnett et al. 2013). Octopus depredation has been the subject of research on crab and lobster fisheries from the beginning of last century (Garstang 1900), driven by the value of the loss of product as per this research on the southern rock lobster fishery in South Australia (Brock and Ward 2004; Hunter et al. 2005; Harrington et al. 2006; Briceño et al. 2015).

Most octopuses are generalist predators, displaying an opportunistic feeding behaviour strongly linked to prey abundance and environmental conditions (Boyle and Rodhouse 2005). Adult lobsters and crabs caught in traps are unable to escape from foraging octopuses which are able to easily enter traps and kill individuals before they are harvested by fishers. Depredation risk by octopus is difficult to predict given strong inter-annual variation in octopus abundance, particularly within areas that experience extreme temperature variation (Garstang 1900; Rees and Lumby 1954). Additionally, crustacean fisheries can be affected by the consumption of bait by octopus in lobster traps because

this prevents subsequent lobster capture (Smith 2003; Groeneveld et al. 2006). Despite the economic impacts of lobster mortality and bait consumption, effects of octopus predation have been underestimated in many fisheries (Groeneveld et al. 2006) and its quantification and incorporation into stock assessments of lobster fisheries is spatially and temporally limited (Briceño et al. 2015).

3.3.1 The octopus–rock-lobster fishery interaction in South Australia

The South Australian rock lobster (*Jasus edwardsii*) fishery (SARLF) has a gross value of $86.1 million from 1,552 tonnes of production (2012/2013) (ABARES 2014). The SARLF is divided into two management zones – the northern and southern zones – with the latter being the most productive zone (Linnane and Crosthwaite 2009; Linnane et al. 2014a,b). Approximately 98% of total in-pot lobster mortality in the SARLF is due to predation by the Maori octopus (*Pinnoctopus cordiformis*, also known as *Octopus maorum*, O'Shea 1999) (Brock and Ward 2004), which is the largest octopod in Australasia (Norman and Reid 2000). Lobster mortality and octopus catch through time are highly correlated in the SARLF (Linnane et al. 2014a,b) suggesting that in-pot octopus predation is influenced by trends in octopus abundance. Additionally, octopus depredation risk decreases with depth so that there is greater impact in inshore SARLF areas (<60 m depth) (Brock and Ward 2004). Between 1993 and 2013, a total of 3,289,538 lobsters were reported killed by octopus (<60 m) in the SARLF (average 164,000 per year; supplementary information, Figure S3.1) with large spatial and temporal variation (Linnane et al. 2014a,b). Additionally, although the current investigation concentrates on South Australia, the interaction between *P. cordiformis* and *J. edwardsii* within fishing gear is also known to lead to significant economic losses elsewhere including in Tasmania (Hunter et al. 2005; Harrington et al. 2006; Briceño et al. 2015) and New Zealand (Ritchie 1972).

Data on lobster size are collected through routine fisheries research programs and this has shown that the size of lobsters killed by in-pot predation has been decreasing over recent years and is now converging on the minimum legal size (MLS) for lobsters (Figure 3.1). It is uncertain how this trend may impact the fishery, although we note the current stock assessment model is length based

(carapace length) and thus there is capacity to include changes in size-specific mortality (Hobday and Punt 2001) in assessments and harvest strategy evaluation. Consequently, a finer examination of key lobster demographic traits, such as size and sex are needed to understand octopus depredation in the SARLF. In addition, the nature of interactions between lobster catch and depredation within fishing gear warrants research because complex patterns have been observed elsewhere (Groeneveld et al. 2006; Briceño et al. 2015).

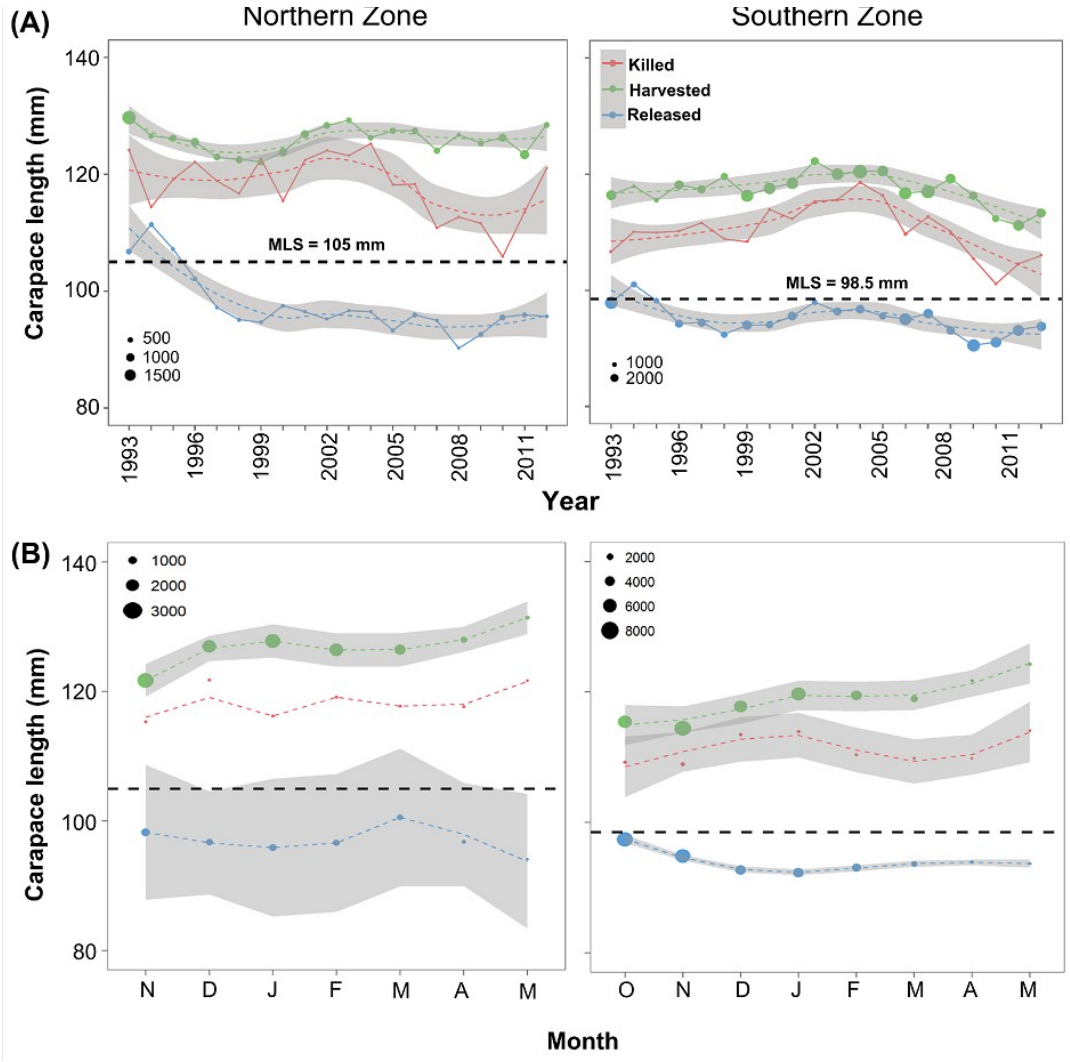

Figure 3.1: (A) Size time series for lobsters killed-by octopus depredation, harvested and released lobsters from the volunteer catch sampling program for the rock lobster fishery in the Northern Zone (NZ) and Southern Zone (SZ) of South Australia. (B) Lobster size distribution at a monthly scale for the same categories. Mean values are represented as circles with circle size representing the number of observations. Dashed lines represent the smoothing (polynomial), and the grey bands represent the confidence interval around the mean (mean + 1.96*sd). Horizontal dashed line represents the minimum legal size (MLS) for each zone.

A depensatory mortality mechanism was suggested to explain the inverse relationship between in-pot lobster mortality via octopus depredation and lobster catches occurring homogenously across the stock assessment areas in Tasmania (Hunter et al. 2005). More recently, it's been shown that this relationship is dynamic temporally and spatially (Briceño et al. 2015). Understanding predator–prey interactions in marine fisheries appears as a key component in the implementation of ecosystem-based management (Tyrrell et al. 2011), with the identification of key trophic linkages resulting in a better capacity to model marine fish populations and food webs (Hunsicker et al. 2011).

The present study examines how demographic traits of *Jasus edwardsii*, such as body size and sex affect risk of in-pot predation via octopus depredation, including whether relationships vary spatially. In addition, we examine how lobster catch rates affect predation risk at a daily scale. Here, lobster mortality is used as a proxy of 'in-pot predation risk' for the SARLF, and we provide insights about temporal and spatial components of octopus depredation that could be beneficial for improving fishery management.

3.4 Methods

3.4.1 Southern rock lobster fishery in South Australia

The northern zone (NZ) and southern zone (SZ) fisheries in South Australia are managed using a combination of input and output controls (Linnane et al. 2014a,b), with data and assessment of these zones further subdivided into marine fishing areas (MFAs). Since 1993, the fishery has been controlled by annual total allowable commercial catches (TACCs), which apply separately across each zone and are divided proportionally among licence holders owning individual transferable quota units (ITQs) (Linnane et al. 2014a,b). In 2013, the TACCs in the NZ and SZ were 345 tonnes and 1,250 tonnes, respectively (Linnane et al. 2014a,b). The fishing season runs from November to May in the NZ, and from October to May in the SZ. Seasons for both zones are referred to here by start-of-season year (Linnane et al. 2014a,b). The MLS in the NZ is 105 mm carapace length (CL), whereas in the SZ it is 98.5 mm CL (Linnane et al. 2014a,b). Fishers in both zones may use up to a maximum of 100 pots (Linnane et al. 2014a,b).

3.4.2 Fishery-dependent size sampling

Data on lobster size from 1993 and 2012 were used for this study obtained from a voluntary fishery-dependent sampling program. This program of voluntary catch sampling by commercial fishers and on-board observers has been implemented in the SARLF since 1991, which provides size measurements of legal and undersize lobsters, as well as the number killed through predation (Linnane et al. 2014 a,b). Fishers are encouraged to sample up to three pots per day, while observers sample all pots. Details on sampling effort are provided in Table A.3.1.1 (Appendix A.3.1). All escape gaps in catch sampling research pots are closed to increase catch of smaller lobsters. Fishers and observers are able to easily recognize in-pot octopus predation as lobsters are killed without damage to the exoskeleton, which appears to be ‘sucked clean’ (Joll 1977; Boyle 1986) (Figure S3.2, supporting information).

We used three categories of lobsters: retained or harvested (H), killed (K) and released (R) lobsters, with released lobsters being those that were undersize. Lobster carapace length (CL, mm) was recorded and referenced by day, depth and MFA. The following MFAs were used for each zone (Linnane et al. 2014a,b) : MFA 15, 28, 39, 40, 48 and 49 in the NZ, and MFA 51, 55, 56 and 58 in the SZ (Figure 3.2). These MFAs reflect where >90% of the catch is taken annually (Linnane et al. 2014a,b).

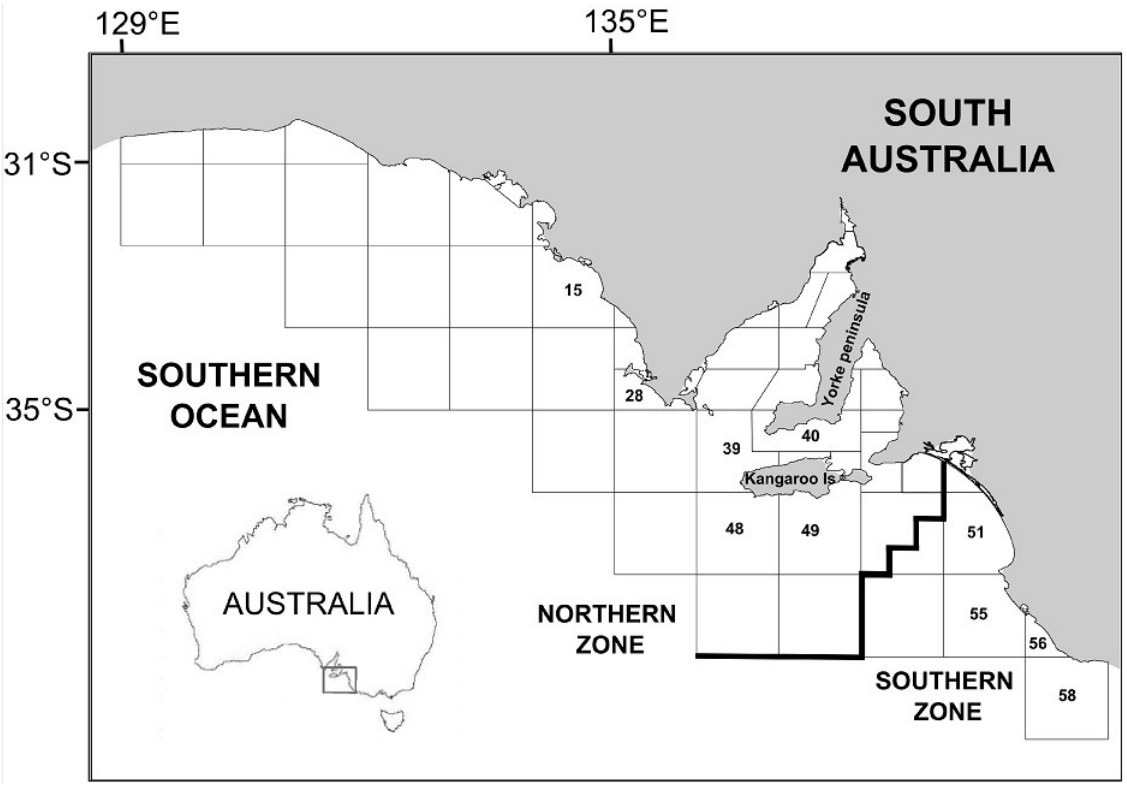

Figure 3.2: Fishing zones (northern and southern) with marine fishing areas (MFA) for the rock lobster fishery in South Australia. The MFAs used for this study are specified with numbers.

Around 90% of catch is taken in inshore areas (<60 m depth) (Linnane and Crosthwaite 2009), where in-pot octopus predation is higher than offshore areas (Brock and Ward 2004). Hence, data used for this study were also standardized by depth (≤60 m). The proportion of lobster killed was calculated as total number killed (K) from the total catch (H+R).

3.4.3 Modelling

3.4.3.1 Testing dependency of life history traits and fishing zones

The relationship between the probability of in-pot lobster mortality and lobster size and sex was modelled using the spatial dependency with fishing zones as predictors. A total of 39,844 lobsters (67.63% female) were included in the analysis considering categories 'H' and 'K' previously described. Sample size was balanced at each temporal and spatial stratum resulting in a balanced design matrix (Table A.3.1.2, Appendix A.3.1), which reduces the risk of bias and ambiguity in linear predictors. Given that temporal changes in lobster size have been documented in both fishing zones (Figure 3.1), we developed a generalized linear mixed model (GLMM) including year as a random intercept, which was nested by zone to reduce the temporal and spatial variability of predictors. The model (Model 1) was selected from a total of five model candidates using as criteria the lowest log-likelihood value, Akaike information criteria (AIC), and degrees of freedom. Further details on model candidates are provided in Table A.3.2.1 and Figure A.3.2.1 in Appendix A.3.2. The binomial probability distribution was given by incorporating 'killed' or 'live' as a binary response, therefore the binomial GLMM (Model 1) was specified as:

Model 1: $P\ (killed) \sim size + sex + zone,\ random = \sim 1 |\ year\ (zone),$

where P is the probability of lobster mortality at given lobster size, sex and fishing zone.

3.4.3.2 Testing density-dependency with lobster catches

A second model (Model 2) was constructed to examine whether the probability of in-pot lobster mortality depended on lobster CPUE. Daily commercial lobster catch (i.e. logbook data) from the selected MFAs was used as an alternative data source. Calculating lobster CPUE from the voluntary program can lead to problems with data dependency (e.g. circularity), thus we utilized commercial CPUE in these models. This dataset was matched with size data by date and depth (≤60 m), which resulted in a total of 35,724 analysed observations. A binomial GLMM was applied using as fixed

predictors size, sex and the interaction between lobster CPUE and MFA. A total of five model candidates were tested, and the selected model was chosen following the same criteria as specified in Model 1. Model candidates and criteria used are provided in Table A.3.2.2 and Figure A.3.2.2 in Appendix A.3.2. The interaction lobster CPUE:MFA was included given the high spatial dependency of lobster catch rate. The temporal variability in lobster catch rate was modelled by including the terms 'year' and 'month' as random factors within the GLMM. This resulted in the following binomial model:

Model 2: $P\ (killed) \sim size + sex + CPUE{:}MFA,\ random = \ \sim 1 |\ (year + month),$

where *P* is the probability of lobster mortality at given lobster size and sex and CPUE:MFA is the interaction between lobster CPUE and marine fishing zones (MFA). Together with the forward step applied to define the GLMM, we tested GLM models for linear predictors exclusively. GLM models showed lower goodness of fit compared with GLMM (Appendix A.3.2). In addition, we further examined temporal components in octopus depredation at inter- and intra-annual (e.g. within fishing season) scales by including year and month as fixed factors in Model 2. All analyses were performed in R using package 'lme4' and 'MASS'(R Development Core Team 2014).

3.5 Results

3.5.1 In-pot predation risk and lobster life history traits

The probability of lobster mortality was dependent upon lobster size, with larger lobsters more likely to be killed (df = 1, F = 28.96, p<0.001) (Table 3.1). In addition, predation risk was affected by lobster sex, with more males killed than females (df = 1, F = 8.25, p<0.01). In-pot predation risk differed among zones, being higher in the SZ than the NZ (df = 1, F = 34.34, p<0.001).

Table 3.1: Parameter estimates from GLMM modelling of the effect of lobster size, sex, and fishing zone on the probability of lobster mortality due to octopus depredation (Model 1).

Random effects				
Parameter	Variance	Std. Dev		
Zone: Year (intercept)	1.850e-02	0.136		
Year (Intercept)	0.015	0.12		
Fixed effects				
Parameter	Value	SE	z-value	p-value
Intercept	-4.61	0.190	-24.23	<0.0001
Size	0.09	0.016	5.77	<0.0001
Sex	0.29	0.054	2.69	<0.01
Zone	0.36	0.063	7.35	<0.0001

3.5.2 In-pot predation risk and lobster CPUE

The effect of lobster catch rate or CPUE on in-pot predation risk varied among MFAs, with significant effects in MFAs 15, 28, 39 from the NZ and MFA 55 in the SZ (p<0.005). The effect of CPUE also varied in direction between MFAs with higher predation risk at low lobster CPUE in northern MFAs 15, 28 and 39 but high predation risk at high lobster CPUE in the SZ MFA 55 (Table 3.2). Moreover, the strength of this relationship varied between MFAs with the highest coefficients in MFA 15 and the lowest in MFA 55. Additionally, the random factors 'year' and 'month' varied 10.6% and 15.4% o respectively, demonstrating that in-pot predation risk varied more at an intra-annual scale (fishing season) than an inter-annual scale.

Table 3.2: Parameter estimates from GLMM modelling of the effect of lobster size, sex, and the interaction between lobster catch rate (CPUE): MFA on the probability of lobster mortality (Model 2).

Random effects				
Parameter	Variance	Std. Dev		
Year (intercept)	0.011	0.106		
Month (intercept)	0.024	0.154		
Fixed effects				
Parameter	Value	SE	z-value	p-value
(Intercept)	-4.05	0.188	-21.50	<0.0001
Size	0.07	0.014	4.74	<0.0001
Sex	0.16	0.057	2.84	<0.01
CPUE: MFA 15	-1.05	0.311	-3.40	<0.001
CPUE: MFA 28	-0.40	0.133	-2.95	<0.01
CPUE: MFA 39	-0.42	0.113	-3.70	<0.001
CPUE: MFA 40	-0.13	0.180	-0.74	0.46
CPUE: MFA 48	-0.17	0.181	-0.93	0.35
CPUE: MFA 49	0.01	0.124	0.10	0.92
CPUE:MFA 51	0.18	0.128	1.41	0.16
CPUE: MFA 55	0.14	0.064	2.20	<0.05
CPUE: MFA 56	0.08	0.052	1.59	0.11
CPUE: MFA 58	-0.05	0.064	-0.74	0.46

Fitted values (Model 2) across years showed spatial variation within in-pot predation with elevated levels of predation risk in specific sites off Kangaroo Island (MFA 48 and 49) and the Yorke Peninsula (MFA 40) (Figure 3.3). Mean fitted values and coefficient of variation (CV%) were 3.02% (CV = 32.7%) for NZ and 4.46% (32.39%) for SZ. Mean fitted values of in-pot predation risk among NZ MFAs were: MFA 49 (4.05%) ~ MFA 40 (4.01%) > MFA 48 (3.27%) > MFA 28 (2.94%) > MFA 39 (2.61%) > MFA 15 (1.56 %). The coefficient of variation (%) of these values also included a spatial component with larger fluctuation among years towards northern areas (e.g. MFA 15, 45.86%). In-pot predation risk for SZ MFAs followed this order: MFA 51 (5.34%) > MFA 55 (5.14%) > MFA 56 (4.45%) > MFA 58 (3.39%). Conversely, inter-annual variability among these areas was more elevated in MFAs 51 and 55 than MFAs 56 and 58.

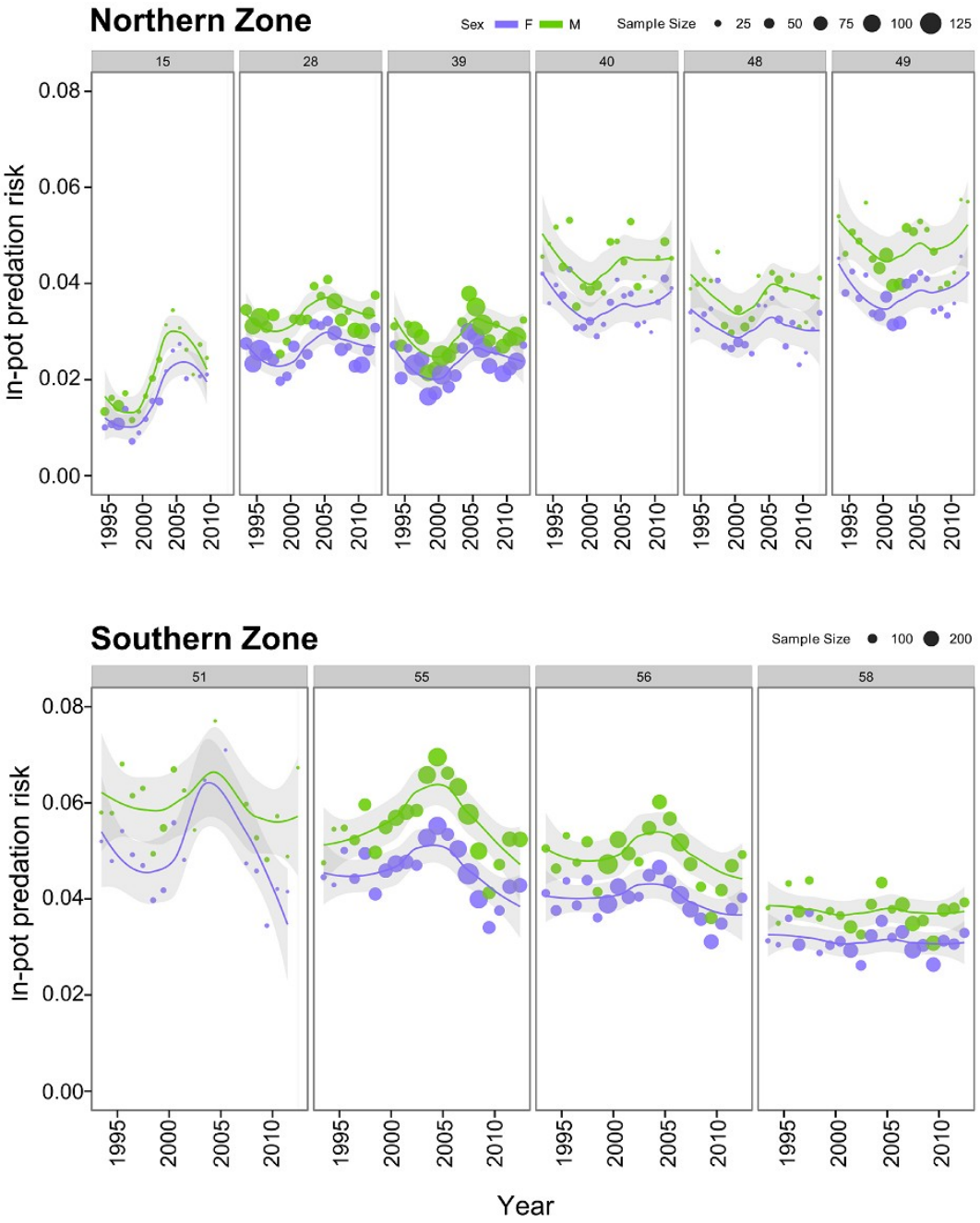

Figure 3.3: In-pot predation risk between 1993 and 2012 from fitted values (Model 2) across selected marine fishing areas from northern and southern zone in the rock lobster fishery of South Australia.

3.5.3 Seasonal trends of in-pot predation risk

An extended version of Model 2 was performed using month as predictor to examine in-pot predation risk across the fishing season (Figure 3.4). We found that predation risk steadily increased across the fishing season in the NZ, with the highest levels close to the end of the season in April and May when catch rate and catch were at their minimum levels (Figure 3.4). While predation risk was

relatively stable across fishing season in MFA 48 and 49, a higher intra-annual variability was found in MFA 15. The seasonal trends in predation risk were broadly similar across all MFAs in the SZ, reaching maximum levels in November before declining over the next three months and rising at the end of the fishing season in April and May.

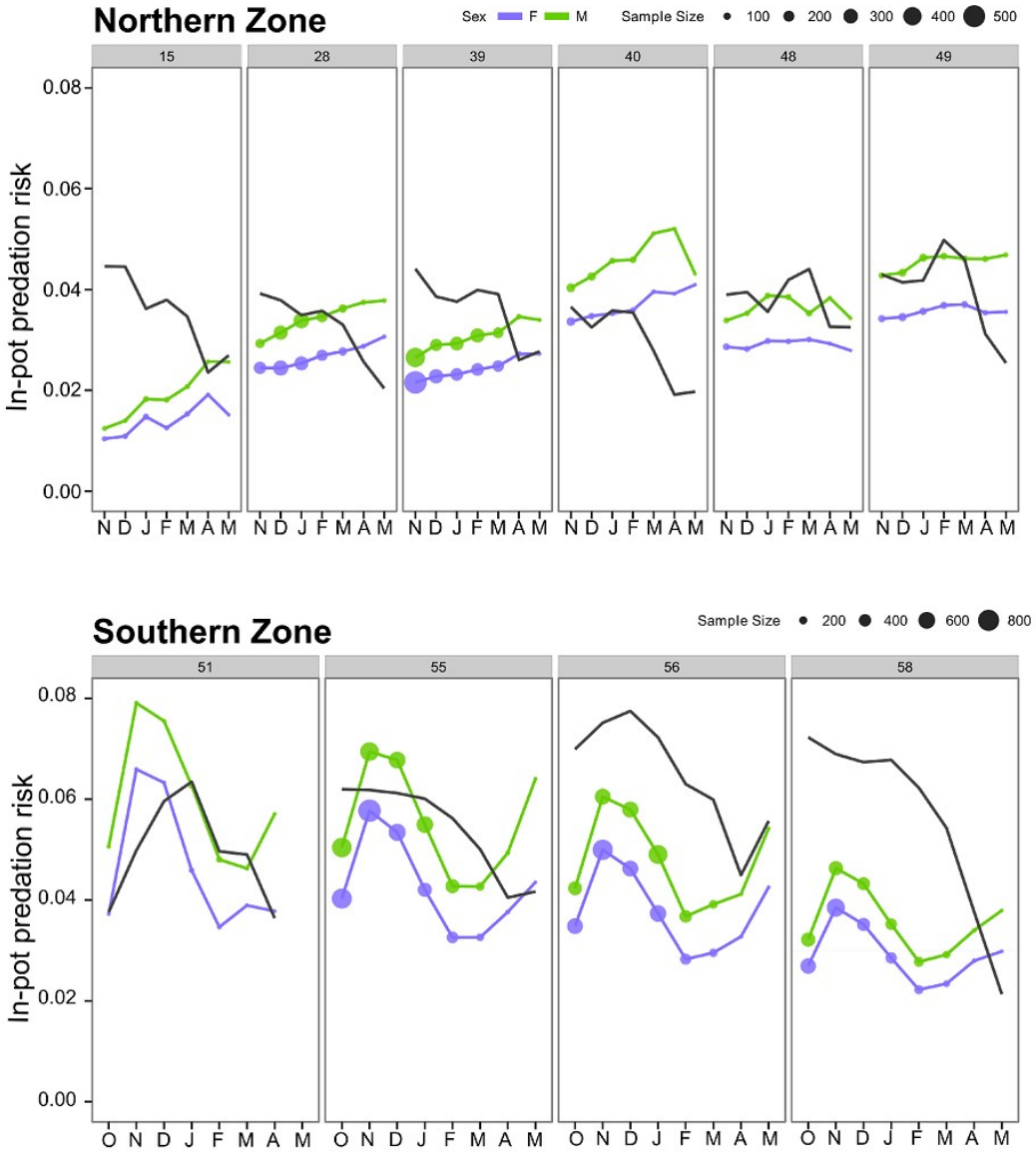

Figure 3.4: In-pot predation risk and lobster CPUE (black line) throughout the fishing season for selected marine fishing areas from northern and southern zone in the rock lobster fishery of South Australia. CPUE was scaled to maximum by zone*sex (max NZ = 1.57 lobster/pot, max SZ = 2.02 lobster/pot).

3.6 Discussion

In this study, we investigated the effect of lobster demographic traits (size and sex) and lobster CPUE on the probability of lobster mortality by octopus depredation in the South Australian Rock Lobster Fishery (SARLF). We found that the predation risk of lobsters was higher for males and increased with size, particularly in the southern zone. Likewise, the relationship between predation risk and lobster CPUE varied at the MFA level, which would suggest different density-dependent mechanisms are affecting the octopus–SARLF interaction in different locations. The relationships among size, sex and density dependencies in lobster mortality in the SARLF were explored, integrating information on fishing factors, lobster ecology and octopus predatory behaviour.

3.6.1 Size and sex dependency of in-pot predation risk

Octopus depredation was higher for larger individuals with males more likely to be killed than females, which is consistent with the findings of a short-term study undertaken in the SZ during the 2000–2001 fishing season (Brock and Ward 2004). Research from a nearby fishery in Tasmania for the same species failed to identify sex-dependant mortality by octopus (Gardner and Frusher 2000), showing broader scale spatial differences in the pattern of octopus predation. Size- and sex-dependent mortality may mirror the catchability and the selectivity of the SARLF. In the Tasmanian rock lobster fishery, larger lobsters were found to have higher catchability than smaller lobsters, and males occur in the pot more often than females due to behavioural interactions (e.g. a dominance hierarchy of agonistic interactions among different-sized individuals) (Karnofsky and Price 1989; Frusher and Hoenig 2001).

3.6.2 Density-dependence of in-pot predation risk

The effect of lobster CPUE on octopus-related mortality in the SARLF differed spatially across MFAs, similar to what occurred in Tasmania (Briceño et al. 2015). We also found that the seasonal

component of fitted values showed higher variation from the predictor 'month' compared with the predictor 'year'. This suggests that there is a predictable seasonal pattern in mortality risk throughout the fishing season and that this pattern is more important than variation from year to year.

Lobster catchability highly depends on feeding behaviour, which is seasonally modified by key physiological and ecological processes such as moulting and mating (Ziegler et al. 2004). Additionally, seasonality of in-pot predation risk could be associated with seasonal changes in octopus abundance on the lobster fishing grounds as reported in some studies (Brock and Ward 2004). For example, coastal octopuses such as *P. cordiformis* perform seasonal migrations to deeper water for reproduction (Robin et al. 2014) which could lead to changes in predatory pressure on lobster.

An inverse correlation between lobster catch rate and in-pot lobster mortality was found in most areas of the NZ. This suggests that a 'depensatory mortality' mechanism may be operating, arising from predator saturation (type II functional response, Holling 1959) and/or from predator avoidance tactics (e.g. 'group-defence' effect; Herrnkind et al. 2001; Hunter et al. 2005). However, depensation in octopus-related mortality was also found here to be affected by lobster size. Catches in the NZ have high variation in lobster size, with larger average sizes towards northern MFAs (Linnane et al. 2014a). This pattern in size of catch may affect octopus predatory behaviour by access to large animals with a low number of individuals per pot (0.02–0.04 lobsters per pot). This is consistent with a recent experimental tank study where the number of attacks by octopus was higher on single lobsters than lobster in groups (Buscaino et al. 2011), likely due to group anti-predator strategies (Herrnkind et al. 2001). Moreover, the octopus hunting strategy is more effective where lobsters are in reduced spaces (Mills et al. 2008; Bouwma and Herrnkind 2009) such as a pot than in the open, which is also known to affect lobster distribution in the wild (Berger and Butler 2001; Butler and Lear 2009). Previous investigations have shown a flexible activity pattern of *P. cordiformis* within lobster pots under experimental conditions in tanks (Brock et al. 2003), although further studies looking at how lobster catchability can be modified by octopus presence as well as others factors involved in killing success deserves attention. For example, the effect of presence of conspecifics of varying size or predators other than octopus on the success of octopus in killing lobsters within traps may be important.

Octopus predation in the SZ followed a different pattern to the NZ as in-pot predation risk increased proportionally with lobster catch rates in MFA 55. MFA 51 and 55 in the northern region of SZ are characterized by catches of small numbers of larger sized lobsters in comparison with MFAs in the southern region (MFA 56 and 58) (Linnane et al. 2008) and this may have contributed to the spatial patterns detected in octopus depredation. A direct relationship between the number of prey consumed and prey density, defined as functional response type I (Holling 1959), assumes that the time spent by predator handling and processing the food is negligible, or that the consumption of food does not interfere with predator food searching. Suitable experiments testing functional and numerical responses in predator–prey interactions are needed in marine fisheries (Hunsicker et al. 2011). Further studies examining predatory mechanism in octopus depredation are relevant in this particular area.

Overall, our findings reveal a significant spatial component in octopus depredation within the SARLF. Inter-annual trends in both fishing zones show a relatively consistent large-scale pattern where lobster killed by octopus depredation increases from the outer-most MFAs towards the two central ones such as MFA 49 and 51. Interestingly, both MFAs are located in areas associated with specific oceanographic conditions such as the upwelling systems occurring around Kangaroo Island (MFA 49) and along the Bonney coast (MFA 51) (Kämpf et al. 2004). These upwelling systems vary seasonally, enhance productivity and aggregate marine life such as small and large pelagic fish (Ward et al. 2004) and marine mammals (Morrice et al. 2004). Such oceanographic conditions could also be beneficial for octopus' populations, although further studies are needed to examine how environmental conditions may enhance octopus settlement.

Spatial variability in predation risk could be attributed to differences among fishing zones in terms of lobster life history (e.g. growth and maturity, McGarvey et al. 1999), environmental conditions (e.g. water temperature, Lewis 1981) as well as habitat type and depth (McGarvey et al. 1999). For example, the spatial heterogeneity in growth of *J. edwardsii* in South Australia is suggested to be a density-dependent process (McGarvey et al. 1999), with higher densities and therefore slower growth, in the SZ compared to the NZ. Higher densities in the SZ appear to be associated with higher levels of puerulus settlement which ultimately translates into higher levels of

fishery recruitment compared to other regions in South Australia. In addition, lobster habitat in the SZ is more continuous, consisting mainly of bryozoan or aeolianite limestone reef, compared with the more discrete and isolated granite outposts found in the NZ (Linnane et al. 2014a). Habitat complexity plays a crucial role in the different ecological traits of lobsters particularly under predation risk (e.g. Eggleston and Lipcius 1992). Additionally, studies have demonstrated that octopus presence can strongly alter distribution and habitat selection in lobsters (e.g. *Panulirus argus*, Berger and Butler 2001; Butler and Lear 2009). Finally, spatial variation in prey density, refuge availability and environmental conditions (e.g. temperature) can strongly constrain octopus foraging ecology and demographic traits (e.g. population size, Robin et al. 2014).

3.6.3 Seasonal models of in-pot predation risk

Whilst lobster mortality steadily increased from November to May in the NZ, in the SZ octopus depredation was elevated from October to November, but then generally decreased until May. Importantly, in the SZ such trends were not directly linked to within-season changes in lobster catch rates as was observed in the NZ. It is unclear whether such seasonal changes in octopus depredation are related to extrinsic (e.g water temperature and food availability) or intrinsic (e.g size and maturity stage) factors related to octopus population dynamics as such information is unavailable. Nevertheless, it is possible zonal oceanographic processes may be affecting the foraging behaviour of octopus. Current understanding of seasonal trends in octopus catch rates by the SRLF is restricted to the SZ, where maximum catches occur at the beginning of the season and then decrease to May (Linnane et al. 2014b). For the SZ fishery, bottom temperatures are low at the onset of summer (Lewis, 1981) as predominantly southeasterly winds drive in the Bonney upwelling where nutrient-rich cold water (11-12°C) intrudes onto continental shelf (McClatchie et al. 2006). It is possible that octopus foraging could be constrained by cold waters during summer months as a function of lower metabolic demands (Moltschaniwskyj and Carter, 2010), as well as by lower lobster availability in pots given reduced lobster catchability during summer months (Fenestra et al. 2014). Future studies examining octopus foraging ecology and population dynamics throughout the fishing season of the

SARLF would benefit from examining the ecological framework for the octopus-lobster interaction, inside and outside fishing gear.

Seasonal changes in octopus depredation are likely to result in important effects on lobster populations as well as to the SARLF. To further discuss potential impacts of in-pot predation risk throughout the fishing season, the following descriptions are provided integrating lobster population information.

3.6.3.1 Northern Zone

In-pot predation risk increased through the fishing season, reaching maximum levels in April and May when lobster catch rates and catches were lowest. Lobster catchability highly depends on the lobsters' feeding behaviour, which is seasonally modified by moulting and mating (Ziegler et al. 2004). The high predation-risk at the end of the season is expected to impact large males given their dominance in pots at this time (Linnane et al. 2014a). Moreover, risk was lower at the beginning of the season which should reduce in-pot predation of spawning females, which are rarely caught after November (Linnane et al. 2014a). Size of lobsters in catches and thus predation risk is affected by market dynamics, with fishers targeting less desirable large, typically male lobsters when supply levels are low such as during winter (McGarvey et al. 2014). For example, during periods of high catch volume in summer, large lobsters are sometimes discarded because a higher unit price is given to smaller lobsters. Smaller lobsters are generally found inshore and thus are targeted in summer. In winter catch rates tend to decrease, the overall catch volume also declines, the market becomes less selective and large lobsters attain better prices (McGarvey et al. 2014).

Depredation is thus another source of removal in addition to fishing that could modify reproductive behaviour as large males are suggested to control access to females in *J. edwardsii* (MacDiarmid 1991). The removal of large males may result in sperm limitation given that only large males can effectively mate with and fertilize large breeding females (MacDiarmid 1991).

3.6.3.2 Southern Zone

High predation risk occurred mainly in November–December, following the opening of the fishing season, plus later in April–May. This may impact on different groups of lobsters given seasonal changes in size and sex catchability. Males moult at the start of the season and are under-represented in the catch until later in the season when catchability of females declines due to moulting and mating (Linnane et al. 2014b). A sex ratio skewed towards females in catches in the first few months of the season increases their risk of predation including ovigerous individuals in January–February (Linnane et al. 2014b). Impacts on females are clearly of interest due to the direct effect on egg production.

3.6.4 Impacts and mitigation actions

This study provides information to broadly quantify losses of lobsters from depredation in the SARLF at MFA levels. Using mean values of in-pot predation risk by zone (Model 2) (NZ = 3.02%; SZ = 4.46%), the additional mortality from depredation in 2012 (Linnane et al. 2014a,b) would approximate 10 tonnes in NZ (TACC = 345 tonnes) and 56 tonnes in SZ (TACC = 1250 tonnes). Assuming a price of AU$55/Kg (ABARES 2014), the financial loss would be AU$ 0.6 million in NZ and AU$ 3.08 million for the 2012 season. In-pot predation risk varies significantly at seasonal and MFAs scales so the economic impact will vary and will be far higher in some years. Furthermore, data used here excluded lobster mortality from offshore catches (>60 m), and did not include additional economic loss associated with bait consumption by octopus (Brock et al. 2003).

Despite considerable economic loss to rock lobster fisheries due to octopus depredation, interactions between octopus and pots are difficult to avoid and are therefore considered to be inevitable in this commercial fishery. Attempts to reduce mortality traditionally include hauling gear early in the morning but there has also been research on reducing mortality through gear modification. This research involved modifications to conventional pots to create two chambers (Brock et al. 2006).

These reduced depredation but were not adopted commercially due to the reduced catches of legal-sized lobsters (Brock et al. 2006).

The findings from this study could contribute to stock assessment of the SARLF. The current fishery model used to assess the performance of the fishery (Hobday and Punt 2001) is not only length based, but is also both spatially and temporally explicit. By identifying how lobster predation is impacted by size, sex, fishing zone and time period, annual estimates of lobster biomass can be considerably enhanced thus assisting sustainable management of this economically important fishery resource. For instance, outcomes from this study could be incorporated into the length-based models by specifying which lobster sizes are more vulnerable to octopus depredation. Additionally, this study may assist by defining spatial and temporal patterns of octopus depredation and could support future discussions on changing any aspects of management of the fishery (e.g. possible temporal or spatial closures if octopus depredation levels were excessive), especially if these involve shifting catch between areas or months.

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3.9

3.10 Supporting Information

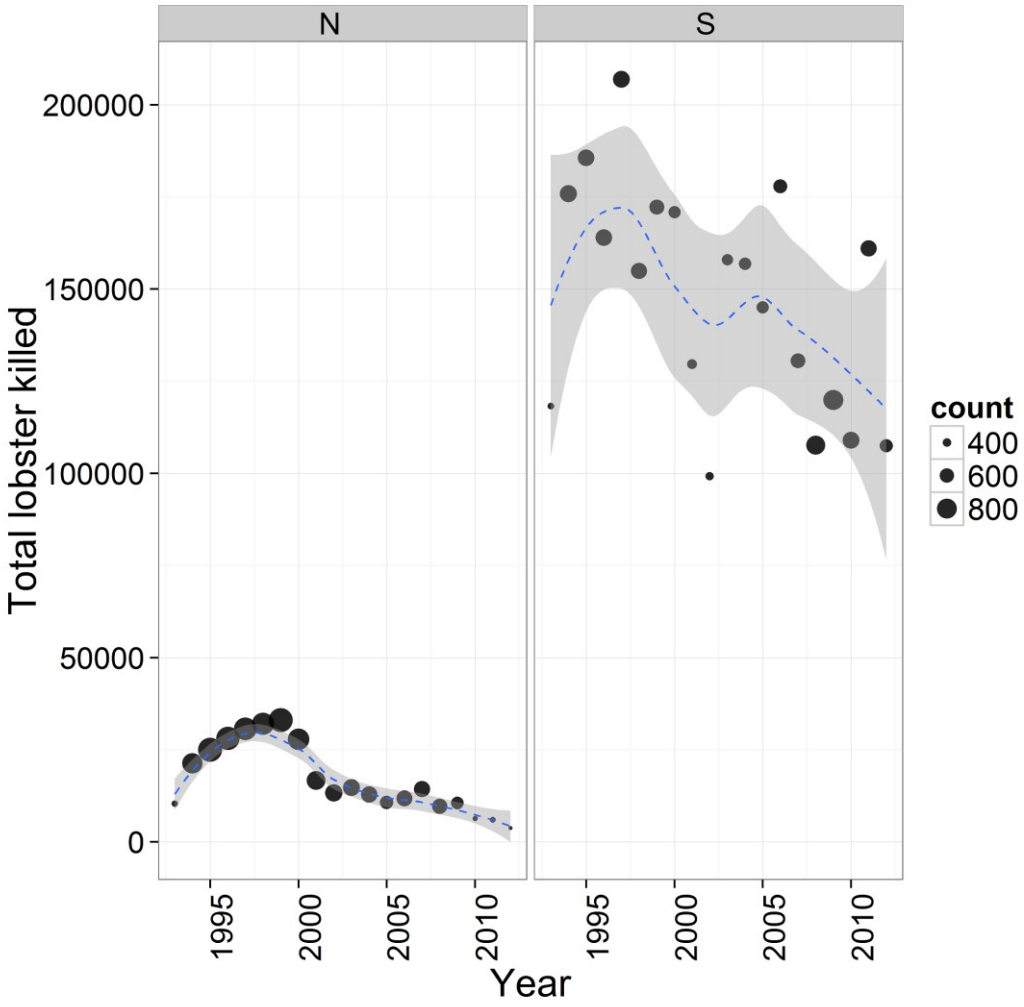

Figure S3.1: Total lobsters killed by octopus within lobster pots between 1993 and 2011 in the northern (N) and southern (S) fishing zone of the rock lobster fishery (*Jasus edwardsii*) in South Australia. Dashed blue black lines represent the smoothing (polynomial), and the grey bands represent the confidence interval around the mean (sum+ 1.96*sd).

Figure S3.2: Lobster killed by an octopus found in lobster trap in Tasmania. The picture shows the characteristic pattern of most of the muscle and viscera removed by the octopus (Felipe Briceño, February 2012)

Appendix A.3.1

Sampling size

Table A.3.1.1: Mean and maximum number of pots sampled per day by year and zone used in this study to examine octopus depredation in the rock lobster (*Jasus edwardsii*) fishery in South Australia.

	Northern Zone			Southern Zone		
Year	**Mean pot/day**	**CV %**	**Max pot/day**	**Mean pot/day**	**CV %**	**Max pot/day**
1993	6.12	77	19	4.79	149	35
1994	3.38	88	16	3.31	138	35
1995	3.55	133	31	3.14	161	34
1996	4.98	76	19	6.31	130	41
1997	3.47	136	29	5.02	159	65
1998	3.23	131	33	3.53	144	33
1999	2.07	51	10	3.97	149	45
2000	1.94	42	5	2.12	38	4
2001	1.90	39	4	1.97	46	4
2002	1.96	38	4	2.16	102	21
2003	1.73	40	6	3.52	165	49
2004	2.16	73	10	4.58	150	41
2005	2.88	119	20	3.76	197	46
2006	2.58	59	11	3.45	174	49
2007	2.01	56	10	2.41	149	42
2008	2.02	99	14	3.06	169	36
2009	3.40	124	28	4.10	193	47
2010	6.94	110	34	4.18	192	55
2011	5.14	143	37	6.27	184	72
2012	3.25	116	20	6.58	205	72

Table A.3.1.2: Total lobsters sampled by year and fishing zone, including sex proportion, used in this study to examine octopus depredation in the rock lobster (*Jasus edwardsii*) fishery in South Australia.

	Northern Zone			Southern Zone			
Year	**Female**	**Male**	**Total**	**Female**	**Male**	**Total**	**Total size**
1993	56%	44%	458	59%	41%	469	927
1994	52%	48%	641	51%	49%	524	1165
1995	56%	44%	664	56%	44%	613	1277
1996	55%	45%	834	55%	45%	1300	2134
1997	53%	47%	604	54%	46%	1201	1805
1998	52%	48%	709	50%	50%	943	1652
1999	51%	49%	632	52%	48%	1692	2324
2000	49%	51%	826	53%	47%	1466	2292
2001	45%	55%	728	54%	46%	1606	2334
2002	52%	48%	606	49%	51%	939	1545
2003	51%	49%	436	54%	46%	1591	2027
2004	50%	50%	485	54%	46%	1850	2335
2005	50%	50%	614	53%	47%	1380	1994
2006	49%	51%	712	52%	48%	2010	2722
2007	50%	50%	560	55%	45%	1866	2426
2008	53%	47%	323	56%	44%	1403	1726
2009	50%	50%	654	51%	49%	1605	2259
2010	50%	50%	944	52%	48%	1297	2241
2011	48%	52%	984	54%	46%	1749	2733
2012	52%	48%	483	56%	44%	1443	1926

Appendix A.3.2

Model selection

Testing dependency of life history traits and fishing zones (Model 1)

Six model candidates were considered (Table A3.2.1). The first step was the selection of fixed factors, and then the random factors. Model selection was performed considering the lowest log-likelihood value (LogLike) and Akaike information criteria (AIC), considering also degree of freedom (df). Two models (M1 and M6) were selected considering a balance between criteria used (Figure A3.2.1). Despite that M3 had the lowest AIC and LogLike we selected M6 because it includes the zone as a nesting process to avoid high variability among fishing zones. By using random effects we can constraint the temporal variation (e.g. year) by zone.

Table A.3.2.1: Model candidates proposed to test dependency of size, sex and zone in lobster mortality by octopus depredation within rock lobster fishery (*Jasus edwardsii*) in South Australia.

LogLike	AIC	df	Model ID	Fixed effects	Random effects
-7541.357	15092.71	5	M1	size + sex + zone	year
-7537.845	15087.69	6	M2	size : sex + zone	year
-7538.507	15089.01	6	M3	size : sex + zone	size(year) – 1
-7536.497	15088.99	8	M4	size : sex + zone	year(zone) + year(size)
NC	NC	9	M5	size + sex + zone	size + year(zone)
-7540.039	**15092.08**	**6**	**M6**	**size + sex + zone**	**year(zone)**

NC: No convergence achieved

Testing density-dependency with lobster catches (Model 2)

Five models candidates were used (Table A3.2.2), considering the same criteria than in model 1. Three models accounted for such criteria (M1, M2 and M5) (Figure A3.2.2). Given that lobster catch rates strongly vary across fishing season (month), we chose M2 because it includes such temporal variation to examine octopus depredation.

Table A.3.2.2: Model candidates proposed to test dependency of size, sex, MFA and lobster catch per unit effort (cpue) in lobster mortality by octopus depredation within rock lobster fishery (*Jasus edwardsii*) in South Australia.

LogLike	AIC	df	Model ID	type	Fixed effects	Random effects
-5311.733	-10653.47	15	M1	GLMM	size + sex + cpue + MFA	Year + month
-5312.515	**-10655.03**	**15**	**M2**	**GLMM**	**size + sex + cpue:MFA**	**Year + month**
-5295.437	-10656.87	33	M3	GLMM	size + sex + cpue + MFA + year	month
-5285.767	-10649.53	39	M4	GLM	size + sex + cpue + MFA + year + month	--
-5312.182	-10668.36	22	M5	GLMM	sex + cpue + MFA + month	size(year)

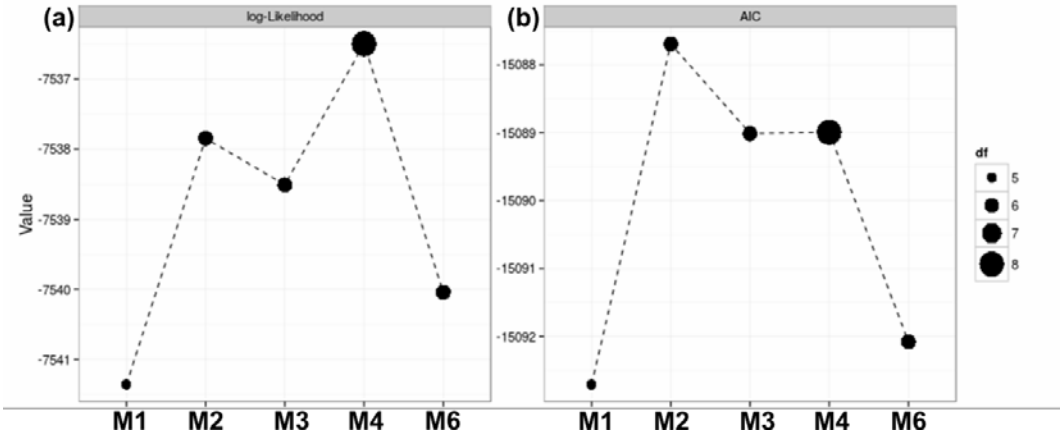

Figure A3.2.1: Model selection criteria based on (a) Log-likehood (b) Akaike information criteria (AIC) used to define Model 1.

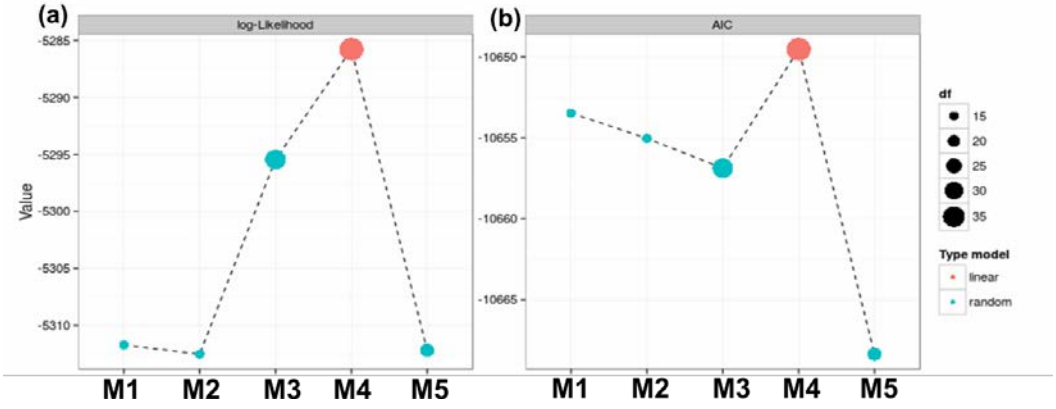

Figure A3.2.2: Model selection criteria based on (a) Log-likehood (b) Akaike information criteria (AIC) used to define Model 2.

Chapter 4:

Physiological responses of lobster under predation risk by octopus

4.1 Abstract

Animals exposed to environments with high levels of predation risk can exhibit a variety of adaptations in terms of morphology, life history, behaviour and physiology. While most understanding of anti-predator responses emerges from a behavioural perspective, little is known about the underlying physiological mechanisms and associated energetic costs. It is commonly observed that an animal under predation threat will increase its metabolic rate or respiratory activity to allocate energy toward escaping behaviours (e.g. 'fight-or-flight'). In this study we tested the metabolic response of lobsters (*Jasus edwardsi*) in the presence of predator (*Pinnoctopus cordiformis*) olfactory cues (kairomones). We examined the circadian pattern of metabolic rates in lobsters using open-flow respirometry. As expected from activity patterns in the natural environment, lobsters showed high routine metabolic rates during the night as they become more active within the respirometer. Therefore night represents the riskiest time of the circadian cycle where (1) lobster energetic demands are increased due to foraging activity and thus (2) increased exposure to predation risk occurs. Hence, we examined the routine metabolic rate of lobsters in response to predator kairomones during the night in order to examine the physiological anti-predator response when lobsters are most vulnerable. Our findings revealed that lobsters strongly reduced their routine metabolism for three hours by 31.4 % when exposed to kairomones in comparison to control values. Here we suggest that lobsters exposed to predation risk during the night reduce their activity to avoid predators; i.e., the anti-predator mechanism is 'freeze' rather than 'fight-or-flight' response. This study provides new insights into the energetic cost of anti-predator responses of lobsters, as well as the ecological and population implications of these responses, with special emphasis on fishing grounds.

4.2 Key words

Predation risk; Fight or flight, ecophysiology, metabolic rates, kairomones, Jasus edwardsii, octopus

4.3 Introduction

Predation can play a key role in the ecological and evolutionary dynamics of populations, as well as in the structure and dynamics of food webs, communities and ecosystems (Murdoch et al. 2003). Population ecology theory has generally conceived predation as a functional response (e.g. predator searching and consuming prey), assuming prey as unresponsive entities (e.g. Murdoch and Oaten 1975). Over the last decades, however, a large body of evidence suggests that prey is anything but unresponsive (Sih 1985; Lima and Dill 1990; Preisser et al. 2005). Here, predation risk or the non-consumptive effects (NCEs) that a predator might exert on its prey can strongly alter key prey traits such as behaviour, morphology, life history and physiology (Lima and Dill 1990; Werner and Peacor 2003; Hawlena and Schmitz 2010; Sheriff and Thaler 2014). These NCEs can have severe, even fatal impacts on prey (Preisser et al. 2005), affecting prey demography (e.g. Zanette et al. 2014), community structure and ecosystem processes (Schmitz 2008; Hawlena and Schmitz 2010;Trussell and Schmitz 2012).

Predation risk can alter organismal physiological nutrient balances by inducing energetically costly stress responses involving hormonal, cellular and metabolic processes (Hawlena and Schmitz 2010b). The general paradigm for predation stress responses (reviewed by Hawlena and Schmitz 2010b) involves increased levels of glucocorticosteroids (hormonal) and heat shock proteins (cellular) resulting in increased cardiovascular activity and increased respiration or ventilation (metabolic) (Slos and Stoks 2008). The increase in metabolism is associated with the 'fight-or-flight' response (e.g. Slos and Stoks 2008) as a consequence of a redirection of energy to locomotory structures to allow an enhanced ability to escape predators (Hawlena and Schmitz 2010b). These stress responses can have substantial consequences for prey, including decreased survival during the stressful episode, inhibition of development and reproduction, slower growth rate and reduced body condition, and reduced assimilation efficiency (conversion of food into body tissue) (Hawlena and Schmitz 2010b). While our current knowledge of prey stress responses under predation risk mostly comes from terrestrial and

freshwater predator–prey systems, very little is known about the physiological response of prey under predation risk in the marine realm (Trussell et al. 2006; Matassa and Trussell, 2014).

In activating physiological mechanisms associated with anti-predator responses, prey must first evaluate the level of risk and the benefit of defence (Kats and Dill 1998; Cooke et al. 2003). 'Sensing' for predator risk reduces uncertainty in prey decision making (Sih 1992) and many animals assess chemical cues from the environment (Kats and Dill 1998) to detect and evade predators (Ferrari et al. 2010). Aquatic crustaceans may rely strongly on water-borne chemicals for assessing predation risk, as is the case for spiny lobsters which can avoid potential predators by detecting chemical cues from key predators such as octopus (e.g. Berger and Butler 2001; Gristina et al. 2011; Buscaino et al. 2011), or alarm cues from injured or killed conspecifics (Shabani et al. 2008; Briones-Fourzán 2009; Hazlett 2011).

The risk allocation hypothesis (RAH) suggests that prey adaptively allocate their foraging efforts and therefore their exposure to predation across high-risk and low-risk situations (Lima and Bednekoff 1999). Additionally, the spatial component in such decision making by prey (e.g. food or shelter) can also involve the selection of areas for foraging (e.g. broad-scale habitat vs patchy habitat) (Sih 1992). For example, feeding rates are higher in open habitats compared with patchy areas where refuges are more abundant, although they represent highly dangerous areas with increased predation risk (Sih 1992). In lobsters the sheltering behaviour appears as an evolutionary trait with predation risk as one of the most important factors altering shelter occupancy (e.g. Weiss et al. 2008).

Trap- or pot-based fishing activities for lobsters enhance their predation risk because these activities can reduce the lobster's capacity to escape predators and the act of fishing can also attract key predators such as octopus. The southern rock lobster (*Jasus edwardsii*) is highly exposed to predation risk by the Maori octopus *Pinnoctopus cordiformis* on fishing grounds in southern Australia (Brock and Ward 2004; Hunter et al. 2005; Harrington et al. 2006; Briceño et al. 2015). Given that the octopus hunting strategy is more effective when lobsters are in confined spaces (e.g. natural shelters) (Bouwma and Herrnkind 2009), octopus predation on lobsters is very successful on individuals confined in fishing traps (Brock and Ward 2004). Additionally, octopus also consume the bait within

lobster traps or pots in some fisheries (e.g. South Australia, Brock et al. 2003; South Africa, Groeneveld et al. 2006) demonstrating the habituation of octopus to the lobster fishery.

It is not known how octopus abundance and predation activity on the fishing grounds can modify key lobster life history traits such as growth, feeding, and reproduction. High-predation-risk environments can generate chronic stress responses to predation risk resulting in reduced assimilation efficiency (e.g. Trussel et al. 2006), decreases in production (growth and reproduction) and altered body nutrient content (Hawlena and Schmitz 2010). Examining the energetic cost of responses to predation risk (e.g. Cooke et al. 2003) is, therefore, a fundamental step in evaluating the stress physiology of lobsters under predation risk. Moreover, quantifying the energetic costs associated with predation will allow a better understanding of how changes in metabolism affect prey at an individual level (Cooke et al. 2003), and propagate through to the population level and ultimately, the function of the associated ecosystem (Hawlena and Schmitz 2010; Zanette et al. 2014).

Spiny lobsters are generally nocturnal foragers, remaining inside their shelter during the day and foraging outside the shelter at night, resulting in a basic circadian pattern in most lobster species (MacDarmind et al. 1991; Weiss et al. 2008). However, such a circadian pattern can be modulated by different intrinsic (e.g. mating behaviour and molting cycle, Childress and Jury 2006) and extrinsic factors (e.g. intense sunlight and moon phase, Childress and Jury 2006) with predation risk being one of the most important selective forces in lobster shelter occupancy (e.g. Weiss et al. 2008). Studies have reported a circadian rhythm in oxygen consumption rates, which is highly correlated with lobster activity demonstrating a strong relationship between behaviour (e.g. movement) and energy expenditure (e.g. metabolic rates) (Crear and Forteath 2000). High metabolic rates are generally associated with activity, highlighting a significant energetic cost of high rates of activity in comparison with resting periods with low metabolic rates. Understanding of the physiological responses of prey individuals under predation risk requires consideration of the circadian rhythm in metabolic rates as anti-predator responses can largely differ between day and night in crustaceans (see Sakamoto et al. 2006).

In this study we hypothesize that lobsters under predation risk increase their metabolic rates according to the general stress paradigm (Hawlena and Schmitz 2010). Using routine metabolism as a proxy of temporal changes in spontaneous activity in lobster respirometry (Crear and Forteath 2000; Kemp et al. 2009; Jensen et al. 2013), first we examined how lobster routine metabolic rate (RMR) is modified along the circadian pattern. We also recreated scenarios of predation risk during the night (a nocturnal scenario) where lobster RMR was examined under presence and absence of octopus odour or kairomones. The current study represents the first attempt in defining metabolic changes associated with anti-predator responses at individual levels in lobsters.

4.4 Methods

4.4.1 Animal collection

A total of 25 inter-moult adult *J. edwardsii* were collected in a scientific reserve with an area of ca. 1 km^2 at Crayfish Point near Hobart in Tasmania, Australia (42°57.2'S : 147°21.2'E). Lobster collection was performed by lobster traps in February (2014), and individuals of both genders measuring up to 110 mm of carapace length (minimal legal size for fishing) were used. In addition, Maori octopus (*Pinnoctopus cordiformis*) individuals (3–6 Kg; n = 3) were collected as by-catch from the same trapping survey. Lobsters and octopus were maintained at the aquaculture facilities of the Institute for Marine Antarctic Studies, University of Tasmania, Hobart, Australia. Lobsters were separated by gender into two rectangular tanks (1,900 L, 2.22 m x 2.05 m x 0.93 m), and provided with concrete building blocks (15 per tank) as shelters. Lobsters were fed with live mussels (*Mytilus galloprovincialis*) three times per week to satiation. Octopus were individually placed in 800-L circular tanks with artificial shelters. Tanks were covered with black mesh to avoid escaping behaviour, and octopus were fed with prawns (*Fenneropenaeus merguiensis*) daily to satiation. Lobsters and octopus were kept at natural ambient temperature (16.5 $\pm$ 1°C) and salinity at 35 $\pm$ 1% with a natural light cycle over two weeks before starting the experiments. Octopus collection, maintenance and handling were conducted under the University of Tasmania Animal Ethics Committee, permit approval No. A0013584.

4.4.3 Respirometry

The rate of oxygen consumption ($\dot{M}O_2$) was measured using an intermittent flow respirometry system as described by Jensen et al. (2013). Two 3.55-L respirometric chambers were immersed in a 455-L tank ('bath') to ensure temperature stability. Each chamber contained an oyster mesh (5-mm mesh size) fitted to the lower section to provide a tractional surface as suggested for crustacean respirometry (Dall 1986). Dissolved oxygen was recorded every 10 s using a luminescent dissolved oxygen optode (Hach LDP, HQ40d, Hach company, USA). Two submersible aquarium pumps

(Quietone 1200) were connected to each chamber. One pump was used to mix the water inside the chamber and to deliver water past the oxygen optode at a rate of 1.0 exchange min^{-1} (3.55 L min^{-1}) (closing cycle). The other pump was intermittently exchanging water between the inside of the chamber and the outside of the chamber at a rate of 1.0 exchange min^{-1} (flushing cycle). A flushing cycle was performed every 10 minutes using a digital timer (DRT-1, Sentinel, China). This resulted in measurements of oxygen consumption every 10 minutes (i.e. 6 measurements h^{-1}) that were averaged to provide hourly means for analysis. Respirometry chambers were carefully rinsed with fresh water after each trial, and sterilized with chlorine after every second trial. During $\dot{M}O_2$ measurement, oxygen levels never fell below 90% saturation to avoid inducing a stress response by the lobsters (Jensen et al. 2013). Background oxygen consumption was measured in empty chambers after each trial for two to four hours as described in Jensen et al. (2013). Lobsters were fasted for 72 hours before any measurement to generate a similar post-prandial state among individuals (Jensen et al. 2013). All respirometry trials were undertaken with two lobsters that were individually and randomly placed into one of the two respirometric chambers.

4.4.4 Circadian pattern in lobster routine metabolism

We defined temporal changes of routine metabolic rates (RMR) associated with the circadian pattern of lobster activity. RMR was measured in inter-moult adults of both sexes (n = 16; 514–732 g) under a natural light cycle with a daylight period of 12–10 hours of light during March–April (2015). A nocturnal cycle approximately between 18:00 and 06:00 was used. The circadian pattern of lobster RMR was examined for 24 hours with trials starting approximately at 12 pm, with each trial considering two lobsters only used once.

RMR was differentiated between night and day as 'RMR_n' and 'RMR_d' respectively. Additionally, the standard metabolic rate (SMR) was also calculated as the mean of the lowest 10% of values following Fitzgibbon et al. (2014). Briefly, SMR represents the energy for maintenance requirements in post-absorptive, non-reproductive, and inactive individuals, measured at a specified

ambient temperature (Careau et al. 2015). Furthermore, this metabolic rate can be determined as the lowest observed values from multiple measurements repeated over a short measuring interval in which measurements of elevated spontaneous activity are excluded (Herrmann and Enders 2007). This experiment was considered as a base line to define a suitable period to add kairomones from octopus taking into account the high metabolism of lobsters, which should be expressed as high activity during trials.

4.4.5 Lobster routine metabolism under nocturnal predation risk scenarios

The effect of predation risk on lobster routine metabolism during the night was examined using predator odour as a kairomone (inter-species chemical cues). This experiment was undertaken using exclusively males (n = 10; 461–769g) between June and July 2014. The exclusion of females was due to the moulting cycle (March–May in Tasmania, Ziegler et al. 2004), which is accompanied by profound physiological changes as recently reported in spiny lobsters (e.g. *Sagmariasus verreauxi*, Simon et al. 2015) and would most likely have influenced our results.

In order to simulate similar environmental conditions to the previous experiment (circadian pattern in lobster metabolic rates), water temperature was kept at 16 $\pm$ 1°C using a titanium heater (2000W, 8.3 A). Lobsters were acclimated for 72 hours at this temperature and deprived of food prior to experimentation. Likewise, octopus were acclimated at the same temperature for 24 hours before placing them into the treatment tank. Three male octopus (4–6 kg each) were randomly used for the trials; the same individual was not used in consecutive trials. In addition, a red light was used to observe lobsters over the nocturnal periods. This was used because these light conditions did not alter the circadian rhythm in other lobster species (e.g. *Panulirus argus*, Weiss et al. 2006).

4.4.5.1 Experimental system

We used an experimental set up that consisted of three main units (Figure 4.1): the conditioning tank (unit A), the treatment tank (unit B) and the respirometric chambers (unit C). Units

B and C were described in the respirometry subsection 4.4.3. The unit A was a circular tank (180 L) used to prepare octopus kairomones. This tank was supplied with water from an open-flow water system mechanically filtered (50 µ cartridge). Unit A was placed approximately 60 cm above unit B, and both units were connected with a PVC tube (50 mm diameter). The water outlet from B was directly discarded allowing an open-water circulation from A to B. In addition, water from the bath was incorporated into the respirometric chambers during the flushing cycles previously described in the respirometry section 4.4.3.

4.4.5.2 Protocol and experimental design

To depict the predation risk scenarios under night time we developed the following protocol (Figure 4.1):

Step 1- Lobster acclimation: Two lobsters were individually placed into each respirometric chamber around 12:00. An acclimation period was established between 12:00 and 18:00.

Step 2 – Kairomone concentration: The concentration of kairomone was created by holding an octopus in the conditioning tank for one hour without water exchange. A 1-h concentration period was used to standardize the accumulation of octopus kairomones without resulting in a deterioration cues as recently demonstrated (e.g. less than one hour, Chivers et al. 2013). Additionally, the concentration period was suitable to minimize octopus excretion, that also may have altered our results, as predator faeces can also act as kairomones (Ferrari et al. 2010). To ensure the lack of predator faeces, octopus were deprived of food for two days prior to experimentation. Furthermore, water condition (i.e. temperature and dissolved oxygen) was monitored in the conditioning tank, where the dissolved oxygen was kept at saturation level (> 90%) using an air stone. After one hour, the octopus was gently removed from unit A and placed back in the maintenance tank used to keep the octopus before this procedure.

Step 3 – Kairomone exposure: The water from unit A containing kairomones was directly flushed into the bath to create an acute kairomone exposure. After flushing, the conditioning tank was

immediately and thoroughly rinsed with fresh water. The open-flow water system was then reconnected allowing the new sea water to flow from unit A to unit B but with no octopus in it.

By using this protocol we assume that (1) lobsters were acutely exposed to octopus kairomones and (2) such exposure was gradually weakened as cues were diluted over the time after reconnecting the open-flow water circulation (Step 3, Figure 4.1). Considering the water exchange in the bath, it was estimated that kairomones remained in this unit for less than approximately 3 hours.

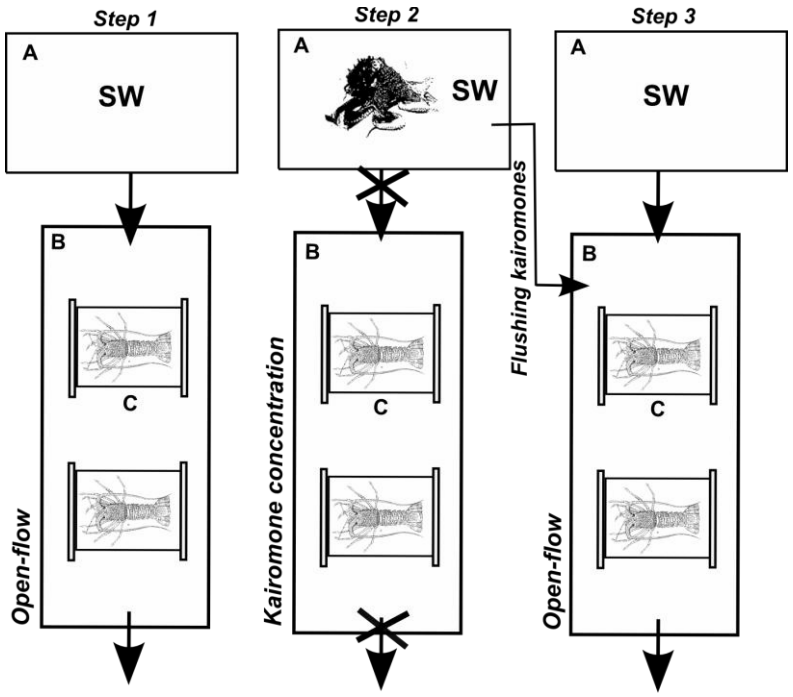

Figure 4.1: Protocol to depict nocturnal predation risk scenarios used in *Jasus edwardsii* adult respirometry. The experimental set up consisted of three units: the conditioning tank (A), the ambient tank or 'bath' (B) and the respirometric chambers (C). The units A and B were connected by an open-flow circulation of sea water (SW) indicated with black arrows. The protocol used to depict the predation risk scenario is as follows: (Step 1) Two lobsters were acclimated for six hours in the unit C with an open-flow circulation. (Step 2) At approximately 23:00 an octopus was held in A for one hour and the open-flow was stopped over this period. Afterward, the SW with kairomones was flushed into B until water volume of A was emptied (Step 3).

Lobster routine metabolic rates were examined during 48-hour trials over two nights (night 1 and night 2, Figure 4.2). Each night we applied one of the two predation risk scenarios: the scenario under predation risk (treatment) or the scenario without predation risk (control). The order of these scenarios was alternated among consecutive trials. The same protocol previously described was used

for the control with the absence of octopus. Each trial consisted of two new animals and lobsters were used only once.

Under the presence of kairomones, RMR_n resulting after kairomone exposure (KE) were differentiated as 'RMR_{nrisk}'. RMR_{nrisk} was examined until the end of the nocturnal period of respirometry (06:00) resulting in a period of six hours after KE.

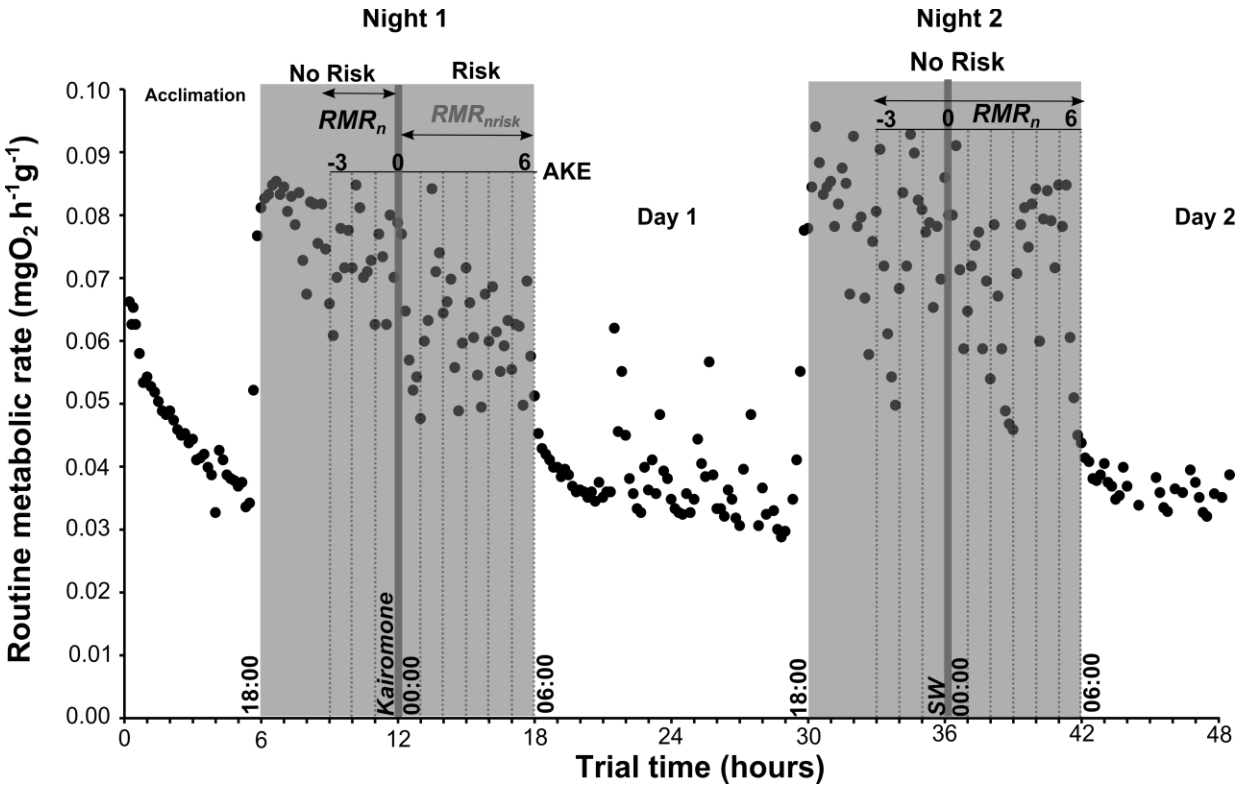

Figure 4.2: Example of a respirometry trial for *Jasus edwardsii* adults (700 g; 17°C) for 48 hours to describe the nocturnal predation risk scenario. Night time is specified by light grey boxes (18:00 and 06:00). Each dot represents one measurement of metabolic rate (mg O_2 h^{-1} g^{-1}) taken every 10 minutes. Routine metabolic rate (RMR) was calculated as hourly mean resulting in six measurements per hour. Nocturnal RMR (RMR_n) was examined over two consecutive nights (night 1 and night 2) where one of the two treatments (absence/presence of kairomones) was applied (approximately at midnight). In this example, a lobster was exposed to octopus cues the first night and the resulting rates after kairomone exposure (KE) (vertical solid lines) were specified as RMR_{nrisk}. On the second night the same protocol was applied but only including sea water (SW) with the resulting rate used as control and referred to as RMR_n.

4.4.4 Data analysis

Metabolic rates and background respiration were determined by linear regressions of the rate of decline in dissolved oxygen concentration for every 10 minutes over the closing cycle. Metabolic rates were expressed in $mgO_2\ h^{-1}\ g^{-1}$ after the subtraction of background respiration. In addition, preliminary observations of $\dot{MO_2}$ in adults of *J. edwardsii* showed a high variability among individuals. Considering such heterogeneity in lobster $\dot{MO_2}$, we applied generalized linear mixed models (GLMMs) including individual lobster identity as a random factor. The circadian pattern of RMR was examined by including the period (day/night) as fixed effect in GLMMs, considering only measurements from control individuals from experiment 1. In addition, temporal changes of RMR under predation risk were examined by including predation risk scenarios (absence/presence of kairomones) and time (e.g. hours KE) as an interaction term (predation risk * time) which was included as a fixed effect in GLMMs.

In experiment 2, GLMMs also considered the inclusion of the order of treatments among nights as a fixed effect. Additionally, the significance of factors was further examined by analysis of variance (ANOVA) with significant differences identified by Tukey's HSD tests for post-hoc multiple comparisons. All analyses were performed in R (R Development Core Team, 2013), using packages 'lme4' for the GLMMs and 'ls means' for Tukey's HSD tests.

4.5 Results

4.5.1 Circadian pattern in routine metabolism

Nocturnal RMR was twice as high as the diurnal RMR (F=163.038, df=159, P < 0.0001) indicating a profound circadian pattern in lobster metabolism (Figure 4.3). Lobsters typically increased RMR_d by 50% between 14:00 and 18:00, and then remained at an average RMR_n of 0.062 ($mgO_2\ h^{-1}\ g^{-1}$) until 06:00. Additionally, RMR_d rapidly decreased between 06:00 and 07:00, which was quite consistent among individuals with a mean RMR_d of 0.038 ($mgO_2\ h^{-1}\ g^{-1}$). The standard metabolic rate (SMR) was 0.03 $mgO_2\ h^{-1}\ g^{-1}$. Overall, RMR_d and RMR_n were 1.3 and 2.1 times higher respectively than SMR.

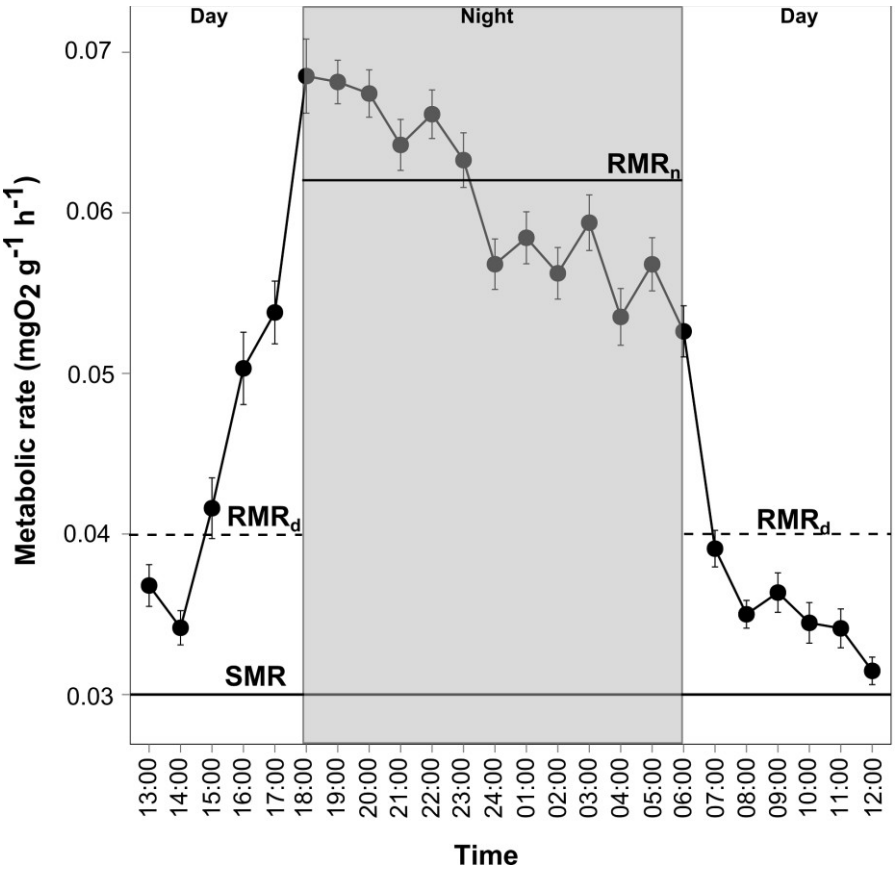

Figure 4.3: Circadian pattern in routine metabolic rate (RMR) in adults *Jasus edwardsii* (n = 16; 514–732 g; 17°C). The grey box represents the nocturnal period between 18:00 and 06:00. Mean values of RMR during night time (RMR_n = 0.062 $mgO_2\ h^{-1}\ g^{-1}$) and day time (RMR_d = 0.040 $mgO_2\ h^{-1}\ g^{-1}$) are specified by the upper (solid) and dashed lines respectively. Mean value of standard metabolic rate (SMR = 0.03 $mgO_2\ h^{-1}\ g^{-1}$) is specified as lower solid line. Vertical solid bars represent mean + 1 se.

4.5.2 Routine metabolism under nocturnal predation risk

Analysis of nocturnal routine metabolic rate (RMR_n) before kairomone exposure showed no variability among individuals (F=0.057, df=6, P=0.818). Lobsters exposed to octopus kairomones strongly reduced their RMR_{nrisk} for three hours by up to 31.42 % (0.02 $mgO_2\ h^{-1}\ g^{-1}$) (Figure 4.4). This response differed significantly between exposed and control lobsters at two (Tukey's HSD, t=3.148, P < 0.05) and three (Tukey's HSD t=3.634, P < 0.01) hours after treatment (i.e., exposure vs no exposure). Furthermore, the reduction in routine metabolism under predation risk resulted in low variability among individuals. Between three and five hours after being exposed, animals rapidly increased their metabolism, reaching similar values to pre-treatment condition. Independently of the treatment, RMR_n was strongly reduced from five hours onwards, demonstrating the effect of time (F=3.89, df=51, P < 0.05), which was close to dawn (06:00). Considering the pattern in RMR observed in treated animals, predation risk can be divided into two periods: (1) RMR decrease over the first three hours, and (2) subsequent RMR recovery with a duration of two hours.

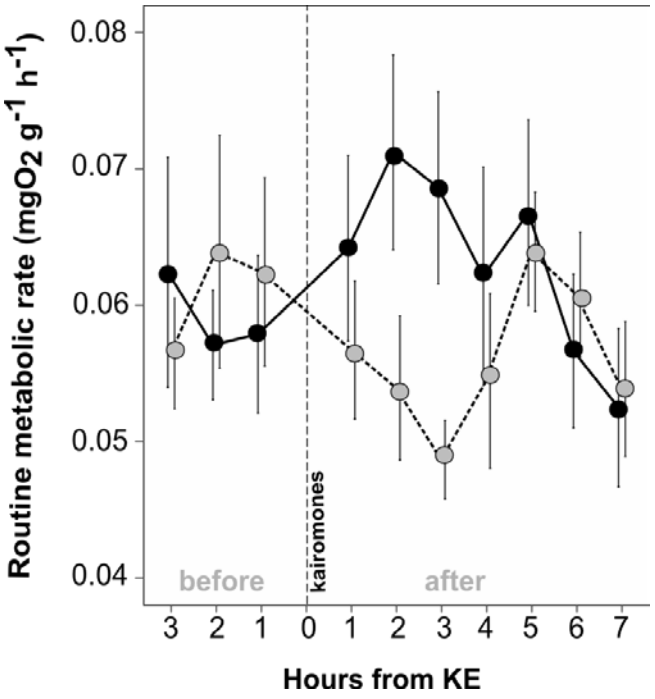

Figure 4.4: Routine metabolic rate of *Jasus edwardsii* adult under nocturnal predation risk scenarios (n=10; 461–769g). The vertical dashed line specifies the time when kairomones (octopus odour) were added (approximately at midnight), here referred as hours after kairomone exposure (KE). Vertical solid bars represent mean $\pm$ 1 se.

4.6 Discussion

In this study we examined the effect of predator kairomones on the routine metabolism of adult *J. edwardsii* as a proxy of the energetic cost experienced by lobsters under predation risk. We report (1) the presence of a circadian pattern in lobster routine metabolic rates and (2) how temporal changes in lobster activity can be altered during night under simulated predation risk scenarios. Our findings demonstrate that, independently of the scenario, lobsters did not increase their routine metabolic rates as we expected in our initial hypothesis, based on the general stress response (Hawlena and Schmitz 2010). Instead, lobsters reduced their routine metabolism by approximately 31% for up to three hours under the nocturnal kairomone exposure. Such changes in lobster routine metabolism under predation risk would be related to a reduction in lobster activity which we hypothesized is an anti-predator mechanism (e.g. immobility). We further expand this hypothesis from an energetic perspective in relation to other anti-predator mechanisms in lobsters (e.g. tail-flipping or 'flight'). Outcomes from this study provide new insights in energetic costs associated with anti-predator responses in aquatic organisms with implications examined at population level.

4.6.1 Circadian pattern in lobster routine metabolism

Changes in light cycle have been demonstrated to play a crucial role in the regulation of activity in lobsters with most demonstrating a circadian rhythm in activity (Childress and Herrnkid 1994; Weiss et al. 2008).

In this study, the nocturnal routine metabolic rate (RMR_n) increased by approximately 50% compared with the diurnal RMR (RMR_d) which is similar to that reported in other lobsters (*Panulirus cygnus*, Crear and Forteath 2001). Major changes in RMR were observed during dusk (18:00) and dawn (06:00) as previously reported in *J. edwardsii* (Crear and Forteath 2000), as well as in other lobsters (*Panulirus homarus*, Kemp et al. 2009; *P. cygnus*, Crear and Forteath 2001). Such changes in lobster activity throughtout the light cycle have been also reported in the field (e.g. MacDarmind et al.

1991) and the laboratory (Williams and Dean 1989) studies in *J. edwardsii*. The circadian rhythm of RMR is suggested to match changes in activity by lobsters within the respirometer (Crear and Forteath 2000, 2001; Kemp et al. 2009). Previous studies in *J. edwardsii* have reported a strong correlaction between activity and metabolic rate by continous observations from respirometer with video cameras (Crear and Forteath 2000). Although we did not perform a systematic observation of lobster activity within the respirometer, random observations during trials confirmed that lobsters become more active during the night and innactive during the day.

4.6.2 Routine metabolism under a nocturnal predation risk scenario

Nocturnal routine metabolism of lobsters was reduced by up to 31.42 % three hours KE in comparison with controls, with RMR_{nrisk} returning to control levels five hours KE. Our findings do not match the general premise of increased respiration or ventilation rates as the first physiological response of prey under predation risk. Instead, we found that threatened lobsters reduced their nocturnal RMR. Similar downgrading of metabolism under predation risk has been reported in arachnids (e.g. Okuyama 2015), fish (Holopainen et al. 1997; Cooke et al. 2003) and tadpoles (Steiner and Van Buskirk 2009). Reductions in metabolism and cardiovascular activity are suggested to mitigate the risk of predation, reducing the need to invest in costly anti-predator responses such as escaping behaviours (e.g. 'flight-or-fight') (Hawlena and Schmitz 2010). In addition, such energetic strategies are suggested to occur in individuals from regions with high predation pressure, which are less likely to waste energy in flight responses, preserving energy to cope with more extreme stress events (e.g. attack) given the abundance of predators as reported in freshwater fishes (Brown et al. 2005; Gravel et al. 2011).

4.6.3 Immobility-or-flight in lobsters?

Predation risk is minimized in lobsters by two major strategies (Herrnkind et al. 2001; Buscaino et al. 2011): (1) 'predator-avoidance mechanisms' (e.g. sheltering or immobility); (2) 'anti-predator

mechanisms' (e.g. escape or weaponry). Such mechanisms, in addition, can operate sequentially as recently reported in some rock lobsters (*Palinurus elephas*, Buscaino et al. 2011). For example, the freezing of a lobster's body as an 'alert posture' during direct encounters with octopus, followed by 'tail-flipping' as the ultimate anti-predator mechanism to move away towards safer areas (Mills et al. 2008; Buscaino et al. 2011). Integrating such information with our results, we have demonstrated that the reduction in lobster routine metabolism under predation risk confirms the immobility response as a predator avoidance mechanism in this species. This can be further supported by studies using octopus as a predator model on decapods in which inactivity is the most common strategy to avoid an encounter with octopus (Table S4.1, supporting information).

Changes in prey activity induced by the presence of a predator's odour are well known across taxa (Kats and Dill 1998), and reduction in prey activity also appears to be associated with the presence of visual predators like octopus (Hanlon and Messenger 1998; Kats and Dill 1998). However, recent advances in our understanding of the octopus olfactory system (e.g. *Octopus vulgaris*, Polese et al. 2015) suggest that chemical signalling can be another source of sensory input that could work in combination with visual cues or alone to provide ecological information especially in light-limited habitats (Nilsson et al. 2012). The role of olfaction in octopus seems to be strongly associated with reproduction (Polese et al. 2015), although previous studies in octopus (Boyle 1983) and cuttlefish (Boal and Golden 1999) have demonstrated that individuals exposed to food odour increases movement (e.g. arousal) and ventilation rates. The olfactory capacity in octopus for prey searching indicates a potential alternative hypothesis to explain the immobility response by lobsters. If *P. cordiformis* is able to detect kairomones from *J. edwardsii* as a target prey, lobster immobility may arise as a strategy to reduce lobster kairomone or metabolites emission in order to remain 'chemically quiet'. Lobsters are hard-shelled animals that store urine and faeces, allowing them to be chemically 'quiet' when necessary (e.g. reproduction, Atema 1995). For example, urine signals can be used during lobster dominance and courtship as chemical cues in the urine are involved with memory (Atema 1995) and individuals can avoid agonistic behaviour by hiding their reproductive status by chemical quiescence (e.g. Diaz and Thiel 2004).

Previous information on chemical ecology among conspecifics should be taken into account for designing experiments to examine lobster physiological responses under predation risk. In this study, each respirometry trial was undertaken considering two lobster individuals that were visually and chemically exposed to the same experimental conditions. *Jasus edwardsii* is a gregarious species during sub-adult and adult stages (Butler et al. 1999), so signals between individuals are biologically/ecologically relevant. The physiological response by lobsters to predator exposure in the wild is also likely to include intraspecific cues. Hence the need for further studies including number of conspecific on lobster physiology as examined in fish respirometry (Herskin 1999).

So far there is little information about the energetic cost associated with either predator avoidance or anti-predator mechanisms in lobsters. Escape response such as tail-flipping is a high-cost energetic behaviour in crustaceans as large muscle fibres that facilitate tail-flipping are involved (England and Baldwin 1983; Jimenez et al. 2008). The dependency on anaerobic metabolism results in an oxygen debt which must be aerobically recovered (Jimenez et al. 2008). We suggest that the lowering of metabolic rates associated with the immobility response may operate as an energetic strategy to avoid investing in a costly escape behaviour such as tail flipping (e.g. 'flight') (Hawlena and Schmitz 2010). Such a strategy can be further examined by recent studies examining the excess post-exercise oxygen consumption (EPOC) as proxy of energetic cost and recovery in lobsters (e.g. *S. verreauxi*, Jensen et al. 2013). Lobsters required around 8.36 $mgO_2\ g^{-1}$ and more than 10 hours for recovery following tail-flipping until exhaustion, representing around 1.2 times the standard metabolism needed during such recovery a period (Jensen et al. 2013). Using such proportion, we further examine our findings by comparing the daily energetic cost needed for standard (e.g resting) and routine metabolism (e.g activity) in the absence of and in the presence of predation risk, as well as EPOC from Jensen et al. (2013) (using caloric equivalent 1 $mgO_2\ g^{-1}$ = 14. 3 J mg^{-1}; Lucas 1993) (Figure 4.5).

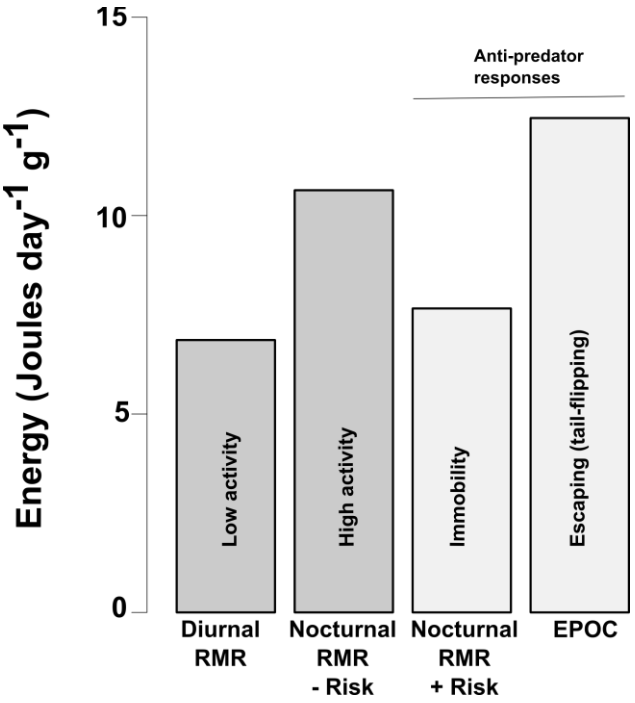

Figure 4.5: Daily energy requirements for lobster activity using routine metabolic rate (RMR) at two levels from circadian pattern in RMR (diurnal and nocturnal RMR), including two anti-predator mechanisms such as (1) Immobility from the lowering in nocturnal RMR under predation risk (+ Risk) here reported, and (2) escaping or tail-flipping from Jensen et al. (2013). Diurnal and nocturnal RMR were calculated assuming 12 h day – 12 h night period. RMR under risk was calculated as 31.4 % of nocturnal RMR (- risk), assuming to be constant over nocturnal period (12 h). The escaping response, in addition, was calculated using the excess-post exercise oxygen consumption (EPOC) from Jensen et al. (2013), representing the energy required for a single escaping event performing tail-flipping until exhaustion (see Jensen et al. 2013).

According to our estimations, a single event of escaping until exhaustion would 'cost' 17.5% more than the usual energy required for nocturnal activity assuming a period of 12 hours. The immobility response may therefore represent a 'saving' strategy compared with tail-flipping, although it would imply around 50% of the nocturnal period under inactivity. The activation of both anti-predator strategies (immobility or flight) may depend on the type of cues (e.g. chemical and/or visual) and/or on kairomone concentrations, as previously suggested across taxa (Lima and Steury 2005), with a greater perceived risk likely resulting in a flight response. Although in this study kairomones were not quantified to recreate the predation risk scenarios, under the experimental conditions here tested *J. edwardsii* did not perform tail-flipping as the main anti-predator response.

4.6.4 Ecological implications

In an ecological context, prey individuals must simultaneously balance feeding and anti-predator demands (Sih 1985; Lima and Dill 1990; Sih 1992). For example, and according to the RAH, individuals experiencing high levels of predation risk would increase anti-predator responses (Lima and Bednekoff 1999). Although we compared both anti-predator mechanism strategies from an energetic point of view, such strategies are equally effective in reducing the lethal effect of predation. The activation of one or the other may depend on habitat conditions such as proximity to refuge areas (Sih 1992). For example, lobsters feeding in open areas (e.g. where shelter availability is limited, Sih 1992) could frequently invest more in escaping responses to move away towards safer areas under predation risk (e.g. patchy areas, Sih 1992). Conversely, lobsters feeding in patchy areas under predation risk are expected to increase sheltering behaviour to reduce the risk of encounter with predators. The effects of habitat condition on lobster survival can be even more critical in *J. edwardsii* as field studies have demonstrated that feeding behaviour in this species seems to be restricted to near-daytime shelter (e.g. MacDarmind et al. 1991). Overall, a prolonged period of sheltering would imply changes in key life history traits such as growth, feeding and reproduction as broadly demonstrated in different taxa (Lima and Dill 1990; Hawlena and Schmitz 2010; Zanette et al. 2014). Although habitat type can be determinant in predator-lobster interactions, a combination of biotic (e.g. prey size, predator abundance, and type) and abiotic (e.g. temperature and light conditions) factors will affect the effectiveness of anti-predator responses in *J. edwardsii*. For example, locomotory activity in spiny lobsters is strongly modulated by biotic (e.g. size, conspecific interactions, and moulting cycle) and abiotic factors (e.g. tides and temperatures; Childress and Jury 2006) that can define encounters with predators under certain environmental and ecological circumstances. In this sense, some factors such as temperature can modulate the probability of encounter of lobsters as anti-predator (e.g. escaping responses) and predator (e.g. search and consumption rates) behaviours as recent studies have demonstrated (Dell et al. 2014). Further examination of the effect of biotic and abiotic factors on anti-predator responses in lobsters is needed.

The energetic cost for lobsters under predation risk may be elevated in fishing areas, given high abundance of predators such as octopus. As octopus can be attracted by lobster traps (e.g. baiting, Brock et al. 2003; Phillips et al. 2012), fishing activity is expected to increasing consumptive and non-consumptive effects towards foraging lobsters. For example, octopus depredation within lobster traps might increase the emission of alarm cues from injured or freshly killed conspecifics, reducing lobster activity (Shabani et al. 2008; Hazlett 2011). Likewise, octopus abundance may alter shelter occupancy and shelter selection by lobsters as lobsters may compete for shelters (e.g. *P. argus,* Berger and Butler 2001; Butler and Lear 2009). Future studies on lobster physiological responses under predation risk should involve different physiological indicators to depict a more complete picture at population and ecosystem levels (see Zanette et al. 2014).

The current study determined individual-level information about the modifications to metabolic rate undertaken by lobsters under predation risk resulting in a first step towards understanding NCEs on lobster population. We demonstrated that a unique metabolic response (e.g. general stress paradigm) may not be generalized for *Jasus edwardsii*; instead, different anti-predator responses may arise, depending on the ecological context.

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4.9 Supporting Information

Table S4.1: Behavioural studies using octopus – crustacean interactions as predator–prey models, indicating field (F) or laboratory (L) investigations.

Prey	Cue type	Prey response	Reference
Shore crab (*Gaetice depressu*)	Chemical	Reduction of activity	Sakamoto et al. 2006 (L)
European spiny lobster (*Palinurus elephas*)	Visual, chemical and tactile	Avoidance	Gristina et al. 2011 (L)
European spiny lobster (*Palinurus elephas*)	Visual, chemical and tactile	Avoidance	Buscaino et al. 2011 (L)
Caribbean spiny lobster (*Panulirus argus*)	Chemical	Avoidance	Berger and Butler 2001 (F); Horner et al. 2006 (L); Butler and Lear 2009 (F)
Caribbean spiny lobster (*Panulirus argus*)	Visual and chemical	Shelter occupancy	Weiss et al. 2008
Hermit crabs (*Dardanus venosus* and *Pagurus pollicaris*)	Chemical	Avoidance	Ross and Boletzky 1979 (L) Brooks 1991 (L)

Chapter 5:

Temperature alters the physiological response of lobsters under predation risk

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5.1 Abstract

Changes in prey activity (e.g. foraging/sheltering) under predation risk can lead to profound alterations in physiological responses which in turn impact energy available for growth and reproduction. Temperature is the main environmental stressor determining energetic costs for aquatic ectotherms; however, it is unclear how ecologically and economically important marine species such as *Jasus edwardsii* can alter physiological functions under the combination of predation risk and environmental changes. This current chapter examines the effect of predation risk (absence/presence) in combination with two thermal scenarios based on projections of sea surface temperature under climate change ('warming' and 'ambient'). Different metabolic traits were examined to determine energetic costs associated with (1) maintenance requirements (standard metabolism), (2) routine metabolism, used here as a proxy of lobster activity under predation risk, and (3) escape responses such as tail flipping and excess post-exercise oxygen consumption. Firstly, lobsters under the warming scenario (23°C) required more energy for maintenance compared with lobsters held under the ambient (20°C) scenarios. Secondly, at 20°C lobster routine metabolism was reduced by 23% in comparison with controls when exposed to octopus cues, validating previous findings (e.g. immobility response). In contrast, at 23°C lobsters showed the same pattern in routine metabolism as controls when exposed to the predator cues, suggesting that at elevated temperatures the anti-predator response may be overridden in sub-adults. Outcomes from this study represent new insights on non-consumptive effects on lobster populations under climatic variability, suggesting important implications at population level.

5.2 Key words

Predation risk; temperature; *Jasus edwardsii*; climate change; Australia

5.3 Introduction

Animals need energy to undertake the three main physiologically based activities of biosynthesis (e.g. growth, gamete production), maintenance (e.g. respiration) and generation of external work (e.g. locomotion) (Careau et al. 2015). High biosynthesis and maintenance costs for an individual are directly linked to increasing food ingestion rates (or foraging) according to the increased-intake energetic model (Careau et al. 2015). In addition, such physiological functions are strongly determined by environmental factors such as temperature (Angilletta et al. 2003; Dell et al. 2014) as well as by ecological contexts such as predator–prey interactions (Cooke et al. 2003; Careau et al. 2008; Killen et al. 2015).

Predator presence can reduce prey foraging rates or increase the use of refugia habitats (Sih 1985; Lima and Dill 1990), negatively affecting both growth and fitness (Trussell et al. 2006; Slos and Stocks 2008). This may cause profound alterations in prey physiology associated with the re-allocation of resources from growth and reproduction to increase survival, causing changes in demographic traits (Zanette et al. 2014) as well as ecosystem structure and function (Hawlena and Schmitz 2010; Schmitz et al. 2010). Likewise, predator attacks increase energetic costs of prey individuals as the escape response is fuelled anaerobically, implying long-term recovery periods (Cooke et al. 2003; Killen et al. 2015). Examination of physiological and behavioural traits across different environmental and ecological stressors, such as predation risk is required to achieve a better understanding of community and ecosystem functioning (Matassa and Trussell 2014). This is especially the case in regions experiencing rapid changes in ecosystem structure and function as a result of increased drivers of climate change (Bozinovic and Pörtner 2015).

Changes in predator–prey interactions, as a function of ocean warming, are resulting in considerable challenges for biological as well as human systems, particularly in regions experiencing significant warming such as south-eastern Australia (Hobday and Pecl 2014). The south-eastern Australian region is one the fastest warming regions in the southern hemisphere (Hobday and Pecl 2014). In Tasmania, warming temperatures have facilitated increased larval survival and settlement of a habitat-modifying sea urchin (*Centrostephanus rodgersii*) resulting in the formation of urchin

barrens, i.e. reef areas that have been stripped of most algae (see Ling et al. 2009; Johnson et al. 2011). This has created structural and functional changes across multiple ecosystem levels (Ling et al. 2009; Johnson et al. 2011), with uncertain implications for key ecologically and economically important species such as the southern rock lobster *Jasus edwardsii* (Pecl et al. 2009; Johnson et al. 2011). *Jasus edwardsii* plays a key ecological role on Tasmanian rocky reefs as it helps control the numbers of this urchin as large lobsters are a key sea urchin predator (Ling et al. 2009). Nevertheless, lobster capacity to control urchins has been decreasing as the abundance of lobsters, and consequently larger lobsters, has declined (Ling et al. 2009).

The ecosystem service that lobsters provide to Tasmanian rocky reefs may also be affected by direct (consumptive) and indirect (non-consumptive) effects of key *J. edwardsii* predators such as the Maori octopus (*Pinnoctopus cordiformis*). As an example of non-consumptive effects (NCEs), lobsters can alter key behavioural traits once exposed to octopus presence, affecting lobster habitat selection and increasing sheltering behaviour (Berger and Butler 2001; Mills et al. 2008; Butler and Lear 2009). In addition, recent studies have demonstrated that octopus presence can also alter *J. edwardsii* physiology; for example, metabolic rates (see Chapter 3). Threatened individuals reduced their metabolic rates (oxygen consumption) for around three hours after being exposed to octopus olfactory cues, used here as a proxy of predation risk. The study hypothesized that lowered metabolic rates of threatened lobsters would reflect a reduction in activity (immobility), a predator avoidance mechanism commonly known in aquatic crustaceans (Hazlett 2011). Such a match between physiological (e.g. reduced metabolic rate) and behavioural (e.g. inactivity) traits has been reported in different taxa (Holopainen et al. 1997; Cooke et al. 2003; Steiner and Van Buskirk 2009; Krams et al. 2013; Okuyama 2015), providing an alternative to the expected general stress response of 'fight or flight' (Hawlena and Schmitz 2010). However, such physiological responses have not been examined further in the context of other key intrinsic and extrinsic factors such as lobster size and temperature which could be pivotal in understanding physiological responses under predation risk in *J. edwardsii*. Projections based on A1F1 scenarios (IPCC 2007) suggest an increase in SST of approximately +3°C by the year 2060 in the south-east Australian region (IPCC 2007; Pecl et al. 2009). Such temperature

increase would impact lobster demographic traits such as growth and abundance, with implications for lobster fisheries (Pecl et al. 2009).

The trade-off between foraging activity and predation risk can be strongly moderated by environmental stressors such as temperature (Killen et al. 2013; Culler et al. 2014; Matassa and Trussel 2014), as the energetic demands and foraging rates in ectotherms are largely influenced by the physiological effect of temperature (Angilletta et al. 2003; Dell et al. 2014). Under warming temperatures, the amount of energy required by prey for maintenance or survival is expected to increase, with implications for individual energy reserves (Hawlena and Schmitz 2010; Schmitz et al. 2010). This may be more intense in juveniles and sub-adults, as growth is one of the main physiological functions. Hence, temperature may be an important but under-appreciated component of prey decision making under predation risk (e.g. foraging vs safety, Sih 1985).

Decision making by the prey (e.g. foraging vs sheltering) can also differ throughout life stages as sheltering is inversely correlated with body size (Sih 1985). For instance, studies in juvenile lobsters (*Homarus americanus*) have demonstrated that lobster size matters in sheltering/foraging behaviour, with smaller juveniles showing a stronger sheltering response than larger individuals (Wahle 1992). Furthermore, small juveniles can increase foraging efficiency under risk if refuge areas supply enough food (shelter-based food supply) reducing energetic costs and exposure to predators (Wahle 1992). Spiny lobsters undergo changes in social behaviours (e.g. social aggregations) throughout their ontogeny (Childress and Herrnkind 1996; Childress 2007). As reported for *J. edwardsii* (Butler et al. 1999), spiny lobsters frequently form aggregations in shelters during juvenile and sub-adult stages compared to early benthic stages (e.g. pueruli). Additionally, sub-adults can display a distinct aggregative response to chemical cues from conspecifics, especially from large lobsters, which minimizes predation risk (Butler et al. 1999).

The current chapter represents a continuation of previous studies in NCEs on *J. edwardsii* physiology (see Chapter 3). Using octopus cues as a proxy of predation risk, the current study examined different metabolic traits in small *J. edwardsii* sub-adults (50 – 60 mm of carapace length) related to predator–prey interactions under thermal scenarios based on projected temperatures for the

region (Pecl et al. 2009). Here, two scenarios were defined: ambient (20°C) and warming (23°C) in combination with presence/absence of predator risk. First, energetic maintenance requirements (standard metabolic rates) were evaluated at both temperatures in order to define the energetic 'baseline' of sub-adults. Second, changes in routine metabolism after octopus olfactory cue (kairomones) exposure were examined to test changes in physiological responses (such as immbolity) under the two thermal scenarios. Third, lobster escape responses such as tail flipping were examined by active metabolic rates and excess post-exercise oxygen consumption.

5.4 Methods

5.4.1 Animals

Sub-adult *J. edwardsii* were collected as pueruli (first benthic post-larval stage) from the wild in southern and eastern Tasmania and reared in the facilities of the Institute for Marine and Antarctic Studies (Taroona) between 2011 and 2014. A total of 100 inter-moult individuals (approximately 50 – 60 mm CL) were selected and grouped for three weeks in a large tank (1,900 L) (holding tank) between October and November (2014). The tank was supplied with flow-through water, where water temperature ranged between 15°C and 17°C and the salinity was approximately 34 PSU. Over this period lobsters were fed with live mussels (*Mytilus galloprovincialis*) every two days as suggested by Simon and James (2007). Lobsters were kept at a natural light cycle of 13–15 h day length over this period.

Two male octopuses (*Pinnoctopus cordiformis*) (6–8 kg) were used to create a nocturnal predation risk scenario as described below (section 5.4.3). These individuals were collected from a scientific reserve with an area of ca. 1 km^2 at Crayfish Point near Taroona in Tasmania, Australia (42°57.2'S: 147°21.2'E). Octopuses were individually placed in 800-L circular tanks provided with artificial shelters and covered with black mesh to suppress escaping attempts. Individuals were fed with prawns (*Fenneropenaeus merguiensis*) daily to satiation. Environmental conditions (temperature, salinity and photoperiod) were the same as described for lobsters above. Octopus collection, maintenance and handling were conducted under the University of Tasmania Animal Ethics Committee, permit approval No. A0013584.

5.4.2 Experimental design

5.4.2.1 Thermal scenarios

The current maximum water temperature over summer in northern Tasmania (20°C) was used as a proxy for the maximum temperatures commonly experienced by *J. edwardsii* in Tasmania.

Considering such temperature as a base line, SST projections under the IPCC-A1F1 scenario (IPCC, 2007) for the south-east Australian region for the year 2060 (+ 3°C) resulted in 23°C. Hence, these thermal scenarios were defined as 'ambient' (20°C) and 'warming' scenarios (23°C).

A total of 48 lobsters (n = 48; 50 – 60 mm CL; 50% female) were acclimated to these thermal scenarios between January and March 2015 for between 7 and 14 days, a suitable period to achieve the metabolic acclimation in lobsters (e.g. *Sagmariasus verreauxi*, Fitzgibbon et al. 2014). In order to avoid prolonged acclimation periods and variability among individuals, lobster acclimation was conducted in four consecutive rounds ('acclimation round') considering 12 sub-adults per round. Acclimation rounds were conducted in four 57-L rectangular tanks at a density of three individuals per tank. Tanks were provided with shelters built with oyster mesh (5 mm mesh size) to reduce agonistic behaviour in *J. edwardsii* sub-adults (Carter et al. 2015). In addition, these tanks were supplied with water from an open-flow system from two head tanks (450 L each one) where the experimental temperatures were achieved via two immersion heaters (8.33 A, 2000 W). The tank water volume was exchanged 3.5 times per hour keeping levels of dissolved oxygen at saturation (>90%) and reducing ammonia levels. Dissolved oxygen saturation was also facilitated by installing air stones in each tank. Temperature was monitored every two hours.

Lobsters were fed with fresh mussels (half-shell per lobster) every second day during each acclimation round. Moulting individuals occurred at very low numbers (<5%) over the acclimation round, and they were excluded for respirometry measurements given profound physiological changes in *J. edwardsii* associated with moulting (Simon et al. 2015). Additionally, before any respirometry measurements were taken, lobsters were fasted for 72 hours to standardise the post-prandial state among individuals (Jensen et al. 2013).

Octopus were randomly selected and acclimated at the same experimental temperatures for 72 hours before lobster respirometry was undertaken. This allowed the match between thermal and predation risk scenarios, as well as reduced thermal stress in the octopus. No food was provided over this period to avoid predator diet cues (faeces) as a confounding factor in the predation risk experiments (e.g. Ferrari et al. 2010). Octopus acclimation was performed in a 200-L circular tank

(shelters and covering mesh provided) supplied with water from a circular tank (800 L) in which a heater was installed (8.33 A, 2000 W). Animals were gradually acclimated from normal temperature to thermal scenarios during 72 hours using a warming rate of 0.5 – 1°C per day.

5.4.3 Lobster respirometry under predation risk scenarios

5.4.3.1 Experimental set-up

Respirometry trials were carried out in a recirculating water system designed to expose lobsters to kairomones (octopus odour), which were used as a proxy for predation risk (Figure 5.1). The system consisted of a conditioning tank (200 L) where an octopus was placed, and which was connected to a 455-L treatment tank ('bath') where an intermittent respirometry system was immersed (descriptions in point 5.4.3). Water was recirculated by a pump (12 HyperFlow Water Rio pump, TAAM Inc, USA) supplying a constant flow rate between the conditioning tank and the bath. The water used for respirometry was previously treated by mechanical filtration (e.g. cartridge, 50 µ). In addition, water temperature was kept stable (at 20°C or at 23°C) by a heater/chiller unit (400 W, TECO, model TK2000, Italy). A submersible pump was connected from the conditioning tank to the heater/chiller unit described above to maintain the experimental temperature. The experimental temperature in the bath was kept constant by a heater (Aqua heat 600 W incl. Nema) during the generation of kairomones. The bath was isolated from the exterior with an opaque plastic sheet (10 mm), keeping the natural light conditions (15–13 hours of day length) to promote the circadian pattern of lobster activity. Additionally, an infrared light was installed above the bath allowing the observation of individuals during night time, in particular to confirm lobster activity before kairomone exposure. Such lighting conditions did not alter *J. edwardsii* circadian patterns as previously reported by Mills et al. (2005). Additionally, respirometry was conducted under a natural light cycle, considering the nocturnal period between 20:00 and 8:00.

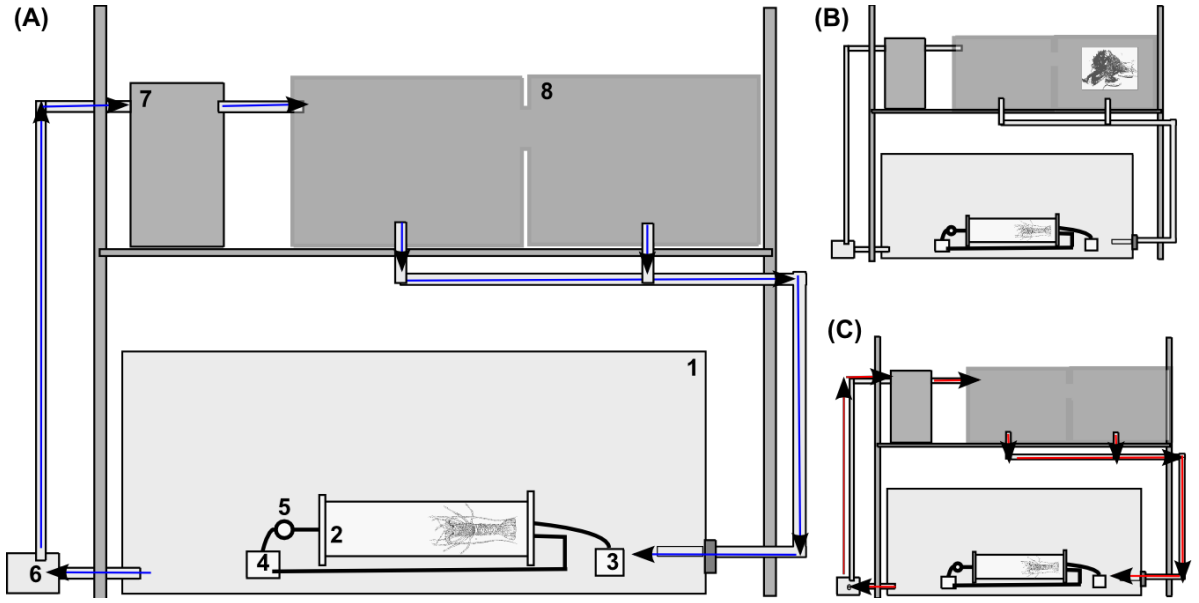

Figure 5.1: (A) Experimental set-up to conduct sub-adult *Jasus edwardsii* respirometry under exposure of kairomones from octopus odour using a recirculating water system. The set-up consisted of the following components: (1) bath reservoir (treatment tank); (2) two respirometric chambers; (3) flushing pump (which pumps water from the bath into the chambers); (4) mixing pump; (5) oxygen probe; (6) recirculating pump; (7) heater/chiller unit; (8) conditioning tank. Lobsters were acclimated for six hours into respirometer before predation risk scenarios (step 1, Table 5.1). Blue arrows show direction of water circulation throughout the experimentl system without kairomones. (B) An octopus was placed into the conditioning tank for one hour to concentrate kairomone (see step 3, table 5.1). (C) Kairomones were directly applied into the bath to initiate the predation risk scenario (Step 4, Table 5.1). Red arrows show the direction of water with kairomones from the conditioning tank to the bath. Kairomones reached the respirometric chambers through the flushing pumps which were close to the discarding point from the conditioning tank. Kairomone remained circulating into the experimental set-up, which were diluted or degraded over the time (step 5, Table 5.1).

5.4.3.2 Respirometry

Measurements of oxygen consumption or metabolic rates ($\dot{M}O_2$) were conducted by an intermittent flow respirometry system consisting of two 3.55-L respirometric chambers. Each chamber had oyster mesh (5 mm mesh size) fitted to the lower section to provide a tractional surface as suggested for lobster respirometry (e.g. Jensen et al. 2013). Additionally an oyster mesh cylinder (15 cm x 7 cm) was included within the chamber to promote sheltering behaviour in lobsters. The dissolved oxygen was measured every 10 s by a luminescent dissolved oxygen optode (Hach LDP, HQ40d, Hach company, USA). Two submersible aquarium pumps (Quietone 1200) were connected to each chamber. One pump was used for mixing the water inside the chamber and delivery of water past the oxygen optode at a rate of 1.0 exchange min^{-1} (3.55 L min^{-1}) (closed or sealed cycle). The flushing cycle was performed every five minutes by connecting the pump to a digital timer (DRT-1, Sentinel, China). This resulted in measurements of $\dot{M}O_2$ every 15 minutes. Briefly, lobsters were placed into

the respirometer around midday and $\dot{M}O_2$ was continually monitored for 26 hours resulting in 104 individual $\dot{M}O_2$ measurements. The first six hours were considered as an acclimation period, which were not included in the analyses. Further details are provided in Section 5.4.4.

Respirometric chambers were carefully rinsed with fresh water after each trial, and sterilized with a chlorine solution every two trials. In addition, oxygen saturation was kept above 90% (e.g. Jensen et al. 2013; Fitzgibbon et al. 2014) and background oxygen consumption was measured in empty chambers after each trial for 3–6 hours. After respiratory measurements, lobsters were removed from the chambers and their wet weight recorded using digital scales ($\pm$0.01 g). Animals were returned to the acclimation tanks until the acclimation round was finished. Over this period, animals were constantly observed and moulted individuals were removed from the analysis.

5.4.3.3 Predation risk scenarios

Nocturnal predation risk scenarios were simulated by the inclusion of kairomones from octopus during lobster respirometry. Two predation risk scenarios resulted from the absence ('- Risk') or presence ('+ Risk') of such predator cues, considered as treatment and control trials respectively. In addition, these predation risk scenarios were randomly undertaken in combination with the thermal scenarios previously described. A protocol describing the steps performed for the generation and exposure of kairomones is shown in Table 5.1. Importantly, the same protocol was applied for control trials, differing only in the presence of octopus in the conditioning tank.

The total number of lobsters used in this study was slightly reduced from the original experimental design (n = 48) given some lobster mortalities (i.e individuals escaping from experimental system) and moulting occurred during acclimation rounds. This resulted in an unbalanced design which is summarized in Table 5.2.

Table 5.1: Protocol used to simulate predation risk scenarios during lobster respirometry in sub-adults *Jasus edwardsii*.

Step	Description
Step 1: Acclimation in the respirometer	(a) Two lobsters were placed into respirometry chambers following the previous description (section 5.4.3.2). Animals were acclimated in respirometry chambers for six hours, generally starting around 12:00 pm (b) Treatment tank and bath are connected through the recirculation pump (Figure 5.1)
Step 2: Recirculation pump off	(a) The conditioning tank was separated from the bath by switching off the recirculating pump, immediately before octopus addition (step 3). Experimental temperature of respirometers was kept as described in section 5.4.3.1
Step 3: Generation of kairomones from octopus	(a) Octopus was taken from the acclimation tank by placing it within a monofilament mesh bag ('onion bag'), allowing an easier addition into the conditioning tank. Such procedure did not result in a stressful condition as inking or abnormal movement were absent. (b) Octopus remained in the conditioningtank for one hour; generally at midnight. (c) Octopus was gently removed from the conditioning tank and placed back into the acclimation tank.
Step 4: Kairomone exposure	(d) Lobsters were exposed to kairomones between 01:00 and 02:00 during highest activity of individuals in the respirometer. We assumed that this first kairomone exposure was highly concentrated; it is considered as an acute exposure. (e) Kairomones were introduced into the respirometric chambers via flushing pumps (see Figure 5.1C).
Step 5: Recirculation pump on	(f) Both sections (conditioning tank and bath) were re-connected by turning the recirculating pump on (as Step 1b). The experimental system remained with recirculation until the end of each trial. (g) This assumes that kairomone was diluted over the time until the end of respirometry.

Table 5.2: Summary of replicates per treatment from thermal and predation risk scenarios used in sub-adults *Jasus edwardsii* (50 – 60 mm of carapace length). Mean body weight and variability (+ se) is included.

Predation risk/Thermal scenarios	Ambient scenario 20°C	Warming scenario (23°C)
Absence (-Risk)	n = 10 (80.60 + 4.24 g)	n = 10 (81.83 + 5.64 g)
Presence (+Risk)	n = 7 (77.43 + 2.75 g)	n =8 (76.75 + 3.29 g)

5.4.4 Metabolic states

The effect of predation risk and thermal acclimation scenarios on lobsters was examined by different metabolic parameters as described in Figure 5.2. These parameters were calculated for each individual with the exception of standard metabolic rate (SMR) as described below. Standard metabolic rate represents the energy for maintenance requirements in post-absorptive, non-

reproductive, and inactive individuals, measured at a specified ambient temperature (Careau et al. 2015); SMR was calculated following Fitzgibbon et al. (2014) as the mean of the lowest 10% of all values exclusively for treatments without predation risk (control trials) under the conditions mentioned above.. The use of percentiles aids to exclude or dilute aberrant measurements associated with technical problems or transient physiological modifications (Clark et al. 2013). In addition, SMR from preliminary trials at 14°C (n = 3) and 17°C (n = 4) under the same respirometry protocol above described allowed a better examination of the relationship between SMR and temperature. Additionally, SMR was further examined by estimating Q_{10} values using the following equation: $Q_{10} = (M_2/M_1)^{10/T_2 - T_1}$ where M_1 and M_2 are SMR at temperatures T_1 and T_2, respectively.

The nocturnal routine metabolic rate (RMR_n) was used as a proxy of nocturnal activity pre and post treatment in relation to kairomone exposure. RMR_n was calculated as the mean hourly $\dot{M}O_2$, examined between 3 hours before and 6 hours after kairomone exposure (KE) (the period between 2:00 and 8:00, referred as 'RMR_{n+risk}'). In addition, diurnal activity was estimated via diurnal RMR (RMR_d) examined over the period between 08:00 and 12:00, resulting in '$RMR_{d\text{-}risk}$' and '$RMRd_{+risk}$' for sub-adults under absence and presence of predation risk, respectively. After 24 hours of the initiation of each trial (approximately between 13:00 and 14:00), each animal was removed from the chamber and swum until exhaustion by manually encouraging the lobster to swim following the method described by Fitzgibbon et al. (2014). This chasing protocol was performed on animals at both predation risk scenarios. Animals were exercised in a circular tank (100 L) for approximately three minutes until lobsters became exhausted and non-responsive to stimuli by hand. Lobsters were immediately replaced in the respirometer and measurements taken to estimate the excess post-exercise oxygen consumption (EPOC). The EPOC was examined at 15, 45 and 60 minutes post-exhaustion. The resulting EPOC for animals under predation risk was referred to as $EPOC_{+risk}$. The active metabolic rate (*AMR*) was defined as the maximum EPOC which generally occurred at the first recording after exhaustive exercise (Jensen et al. 2014; Fitzgibbon et al. 2014). Under the predation risk scenario, this metabolic rate was referred to as 'AMR_{+risk}'. Finally, the aerobic scope (*AS*) was calculated as the difference between *AMR* and *SMR* which was calculated differently for each predation risk scenario. For example, the aerobic scope for individuals without risk ('$AS_{\text{-}risk}$') was

calculated as the difference between AMR_{-risk} and *SMR* which was estimated for each individual. Given the restriction previously described regarding SMR under predation risk, the aerobic scope under predation risk ('AS_{+risk}') was calculated using AMR_{+risk} from each individual but using mean values of SMR (SMR_{mean}) (Figure 5.2b) for each temperature (20°C and 23°C). Hence, these mean values of SMR per temperature were assumed to be the same between individuals under risk.

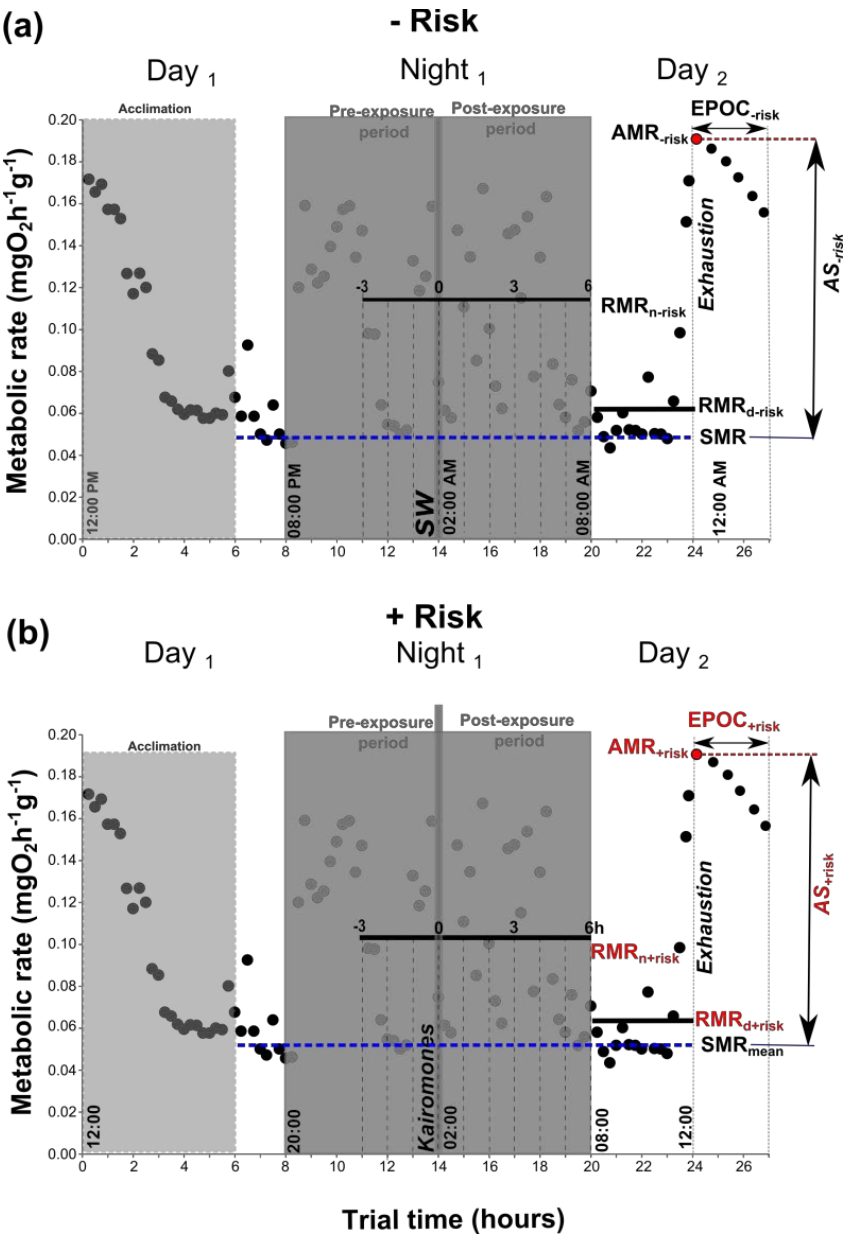

Figure 5.2: An example of a respirometry trial at 23°C showing the levels of predation risk used in this study, (a) absence (-Risk) and (b) presence (+Risk), and the metabolic parameters examined in this study such as the routine metabolic rate during the night time (RMRn) and day time (RMRd), the standard metabolic rate (SMR) and the active metabolic rate (AMR). Additionally, the excess post-exercise oxygen consumption (EPOC) and aerobic scope (AS) is shown. Each dot represents a measurement of metabolic rate over a period of 15 minutes. RMR were calculated as the mean value per hour, and it was examined over two periods: the pre-exposure period (three hours before kairomone exposure) and the post-exposure period (6 hours after kairomone exposure). SMR was estimated as the mean value of the lowest 10% of the measurements and only calculated for lobsters without predation risk. For animals under predation risk, AS+risk was calculated using mean values of SMR (SMRmean) for each temperature. This assumes that animals under risk had the same SMR by temperature, and AS_{+risk} only differed with AMR_{+risk} which was estimated for each individual. AMR and EPOC were obtained after exhaustion as specified by the dashed vertical line. Additionally, the dashed box represents the acclimation period (6 hours) and the grey box represents the nocturnal period defined between 20:00 and 08:00. The predation risk scenario was generated by exposing the lobsters to octopus (*Pinnoctopus cordiformis*) odour (kairomones) performed approximately at 02:00 as illustrated by the vertical grey line. In the no predation risk scenario, this procedure was performed with sea water (SW) only.

5.4.5 Analysis

Metabolic rates of lobsters and background respiration were determined by applying linear regressions to the rate of decline of dissolved oxygen concentration for every 15 minutes over the closing cycle. Metabolic rates were expressed in $mgO_2\ h^{-1}\ g^{-1}$ after the subtraction of background respiration. The relationship between temperature and SMR was analysed by an exponential regression, with ANOVA to test for significance. Given the imbalance between replicates over these experimental temperatures, a Type II ANOVA was undertaken. Temporal changes of routine metabolism over this period were analysed using generalized linear mixed models (GLMMs) including individuals as a random variable following Zuur et al. (2009). By using this modelling technique the lack of independency (repeated measurements) and the heterogeneity among individuals were addressed.

The effect of predation risk scenarios on RMR_n was examined by including the interaction term 'predation risk * hours after KE', with different GLMMs for each temperature. Temperature was not included as a fixed factor to avoid a masking effect on predation risk scenarios. Additionally, GLMMs were used to examine the effect of predation risk and temperature on the circadian pattern of routine metabolism using the interaction period (day/night) * risk (-risk/+risk). This interaction was examined at 20°C and 23°C independently. Significance of factors was tested with a Type II ANOVA. In addition, the effect of predation risk and temperature on AMR and AS was analysed including the interaction predation risk * temperature in the GLMMs. Outcomes from AMR and AS GLMMs were examined by Type II ANOVA to determine the effect of the fixed factors. In addition, EPOC was examined during the first hour following the methods described by Fitzgibbon et al. (2014). EPOC was compared with pre-exhaustion RMR_d by two-tailed independent t-tests. Significance levels were set at $p < 0.05$, and all analyses were performed in R (R Development Core Team 2014), using packages 'lme4' for the GLMMs and 'car' for ANOVA.

5.5 Results

5.5.1 The effect of temperature on standard metabolism

Overall, SMR exponentially increased between 14°C and 23°C demonstrating a significant effect of temperature on this measure of metabolic rate ($\chi^2 = 37.304$, df = 1, $p < 0.0001$) (Figure 5.3). Coefficients from the SMR–temperature relationship are shown in Table 5.2. Q_{10} values for these temperatures were $Q_{14\text{-}17} = 1.83$; $Q_{17\text{-}20} = 1.54$; $Q_{20\text{-}23} = 2.99$. In particular, SMR increased around 39% between 20°C and 23°C showing a relatively similar variability (coefficient of variance, CV= 21%).

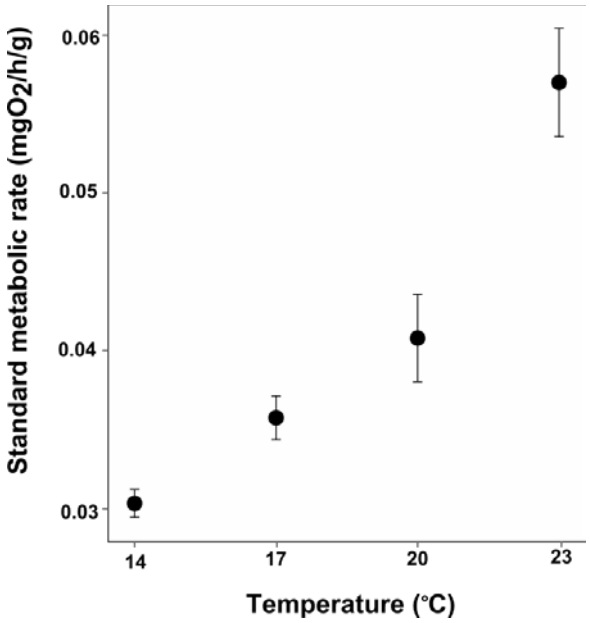

Figure 5.3: (a) Mean values of standard metabolic rate at 14°C (n = 3), 17°C (n = 4), 20°C (n = 10) and 23°C (n = 10) for sub-adults *Jasus edwardsii*. Vertical bars represent standard errors.

Table 5.3: GLMM coefficients describing the relationship between temperature (14–23°C) and standard metabolic rate of *Jasus edwardsii* sub-adults (body weight = 79 g ± 13 g).

Coefficient	Estimate	SE	Df	t-value	p
Fixed effect					
a (Intercept)	0.009	0.23826	27	-19.157	<0.0001
b (Temperature)	0.07127	0.01167	27	6.108	<0.0001
Random effect	Intercept	Residual			
Std . Dev	0.1730043	0.06487662			

5.5.2 Temporal changes in routine nocturnal metabolism after KE

Routine metabolic rate occurring 3 to 1 hours before KE (the pre-exposure period) was similar between predation risk scenarios at 20°C ($\chi^2 = 0.0493$, df = 1, p = 0.8243) and 23°C ($\chi 2 = 0.0493$, df = 1, p = 0.58) (Figure 5.4a). Temporal changes in RMR_n after KE were found at 20°C but not at 23°C resulting in the following three main periods: (1) a quick reduction in RMR_{n+risk} between the pre-treatment period and the first hour after KE at 20°C ($\chi^2 = 4.8012$, df = 1, $p < 0.05$). This decrease in RMR_{n+risk} resulted in a reduction in metabolism of 29% (or a difference of 0.024 $mgO_2h^{-1}g^{-1}$) compared to control animals suggesting an acute response at this temperature. (2) An increase in RMR_{n+risk} between 1 and 3 hours after KE observed at both temperatures without any difference between predation risk scenarios. However, lobsters under predation risk at 20°C consumed approximately 32% less oxygen than controls. (3) A decrease in RMR_{n+risk} between 3 and 6 hours after KE at both temperatures was observed independently of the predation risk scenario. Nevertheless, the rate of decline was slightly more in RMR_{n+risk} than RMR_{n-risk} at 20°C according to the interaction predation risk * hour ($\chi^2 = 3.357$, df = 1, P = 0.067).

5.5.3 Nocturnal and diurnal RMR under predation risk and temperature

RMR_{-risk} at 23°C was approximately 41% higher than at 20°C (Figure 5.4b). Additionally, RMR_{-risk} was reduced during day time by around 20% and 21% at 20°C and 23°C respectively. Under predation risk, animals showed a difference in RMR between periods at 20°C (interaction risk * period, $\chi^2 = 7.0891$, df = 1, $p < 0.01$). For example, mean RMR_{n+risk} was on average 17% lower than mean RMR_{n-risk}, and mean RMR_{d+risk} was 14% higher than mean $RMR_{d-risk.}$ Interestingly, nocturnal routine metabolism under predation risk was not significantly different from the diurnal metabolism of animals in the absence of risk. At 23°C, lobsters demonstrated the same pattern as controls reducing (16%) routine metabolism during the day but without significance between predation risk scenarios ($\chi^2 = 1.3243$, df = 1, p = 0.2498). Further details about the relationship between predation

risk, period and temperature are provided as supplementary information (Table S5.1, GLMM outcomes).

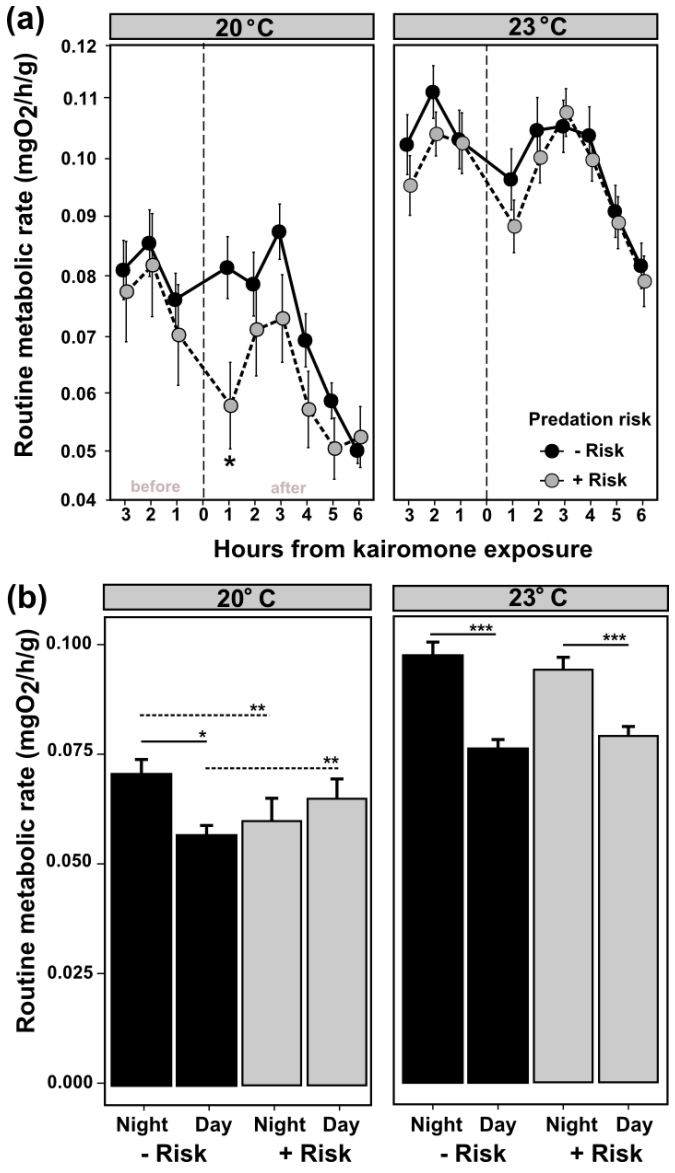

Figure 5.4: (a) Temporal trends in routine metabolic rates (RMR) for sub-adults *Jasus edwardsii* after kairomone exposure representing absence (- Risk) and presence (+ Risk) of predation risk at two temperatures: 20°C and 23°C. Dashed vertical lines represent the time (approximately at 02:00 am) when animals were exposed with kairomones, with 6 hours after the exposure at around 8:00. Significance between treatments (ANOVA test, type II) (- Risk vs + Risk) is expressed by an asterisk. Vertical bars represent individual variability (mean ± 1 SE): – Risk x 20°C (n = 10), + Risk x 20°C (n = 7), - Risk x 23°C (n = 10), + Risk x 23°C (n = 8). (b) Mean routine metabolic rates at day and night for *Jasus edwardsii* sub-adults under conditions of absence (- Risk) or presence (+ Risk) of predation risk at ambient (20°C) or projected warming (23°C) temperatures. Horizontal bars represent intra (solid) and inter (dashed) differences, with asterisks specifying the level of significance: * <0.05, ** <0.01; *** <0.001.

5.5.2 Active metabolic rate and aerobic scope under predation risk and temperature

The mean AMR_{-risk} was around 7% higher at 23°C than at 20°C (Figure 5.5a), although variances between temperatures were similar (approximately 18%). Conversely, lobsters under predation risk had a similar mean AMR_{+risk} between temperatures but differed in that the variance was larger at 20°C than at 23°C ($CV_{20°C}$ = 19% and $CV_{23°C}$ = 7% respectively). Additionally, mean AMR_{+risk} at 23°C was slightly higher than AMR_{+risk} at 20°C, although predation risk did not affect this measure of metabolic capacity. The interaction between predation risk and temperature was not significant (χ^2 = 0.2035, df = 1, p = 0.652), suggesting that, independently of the temperature and predation risk, lobsters consumed a similar amount of oxygen after exhaustion.

There was an inverse relationship between the aerobic scope and the temperature for both predation risk scenarios, resulting in an elevated aerobic scope at 20°C compared to 23°C (Figure 5.5b). Additionally, individuals under predation risk showed a drop of 0.0159 ($mgO_2\ h^{-1}g^{-1}$) between 20°C and 23°C. Furthermore, variability among individuals was higher at 20°C (25%) than at 23°C (11%).

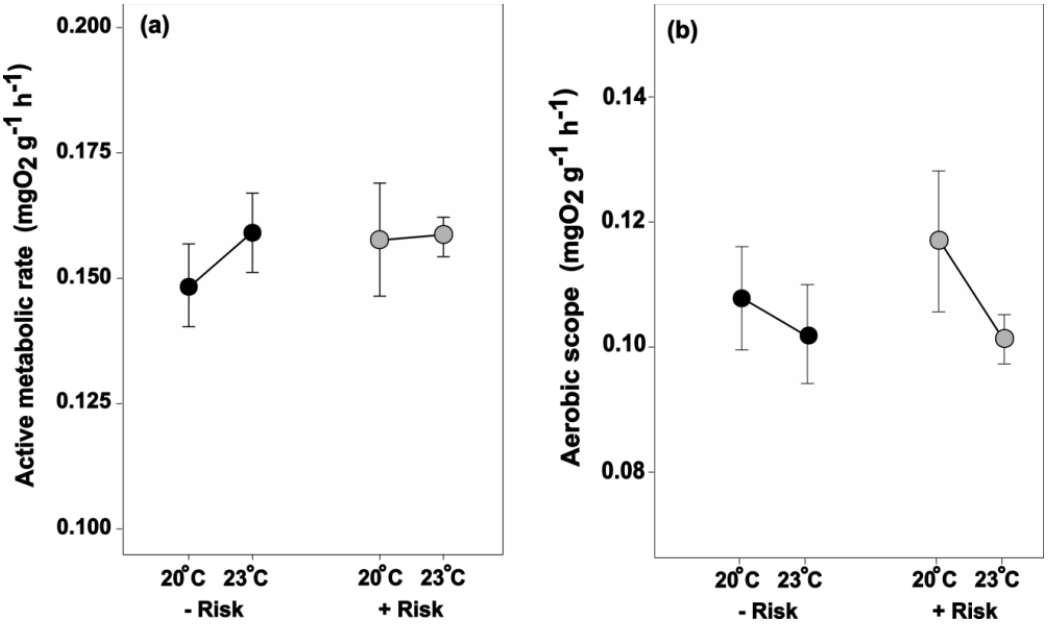

Figure 5.5: Relationship between sub-adult *Jasus edwardsii* active metabolic rate and temperature (a), and aerobic scope and temperature (b) under the absence (- Risk) and presence (+ Risk) of predation risk. Vertical bars represent individual variability (± SE). Vertical bars represent individual variability (mean + 1 se: – Risk x 20°C (n = 10), + Risk x 20°C (n = 7), - Risk x 23°C (n = 10), + Risk x 23°C (n = 8).

5.5.4 The effect of predation risk and temperature on EPOC

There was no difference in EPOC between predation risk levels at 20°C (χ^2 = 0.077,df = 1, p = 0.782) or at 23°C (χ^2 = 0.020; df = 1, p = 0.887). However, temperature strongly affected EPOC (χ^2 = 1327.48; df = 2, p < 0.001), although there was no difference in the temporal patterns in EPOC between temperatures (interaction time * temperature) (χ^2 = 0.569; df = 1; p = 0.4504) (Figure 5.6). Furthermore, EPOC at 20°C and 23°C did not return to pre-exhaustion routine metabolic levels during the examination period (within 60 min after exhaustion).

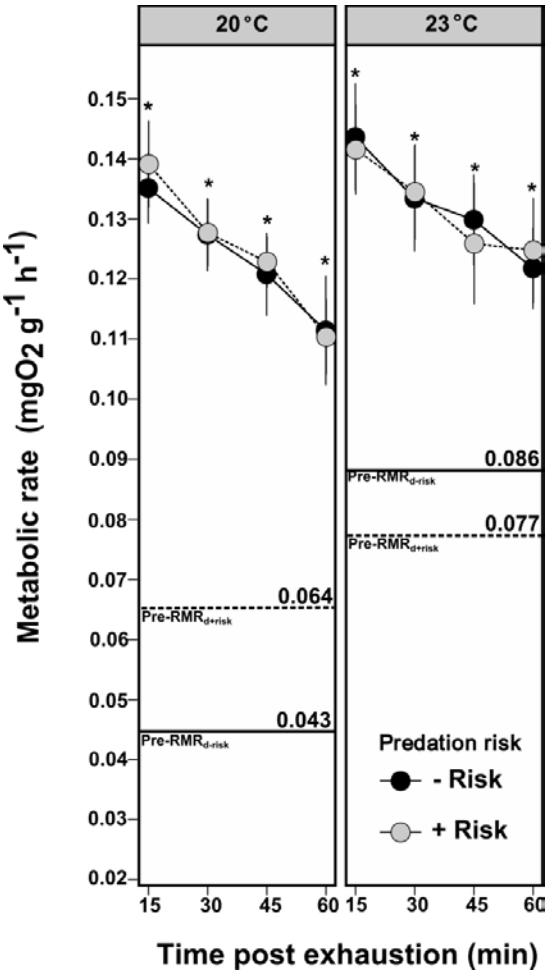

Figure 5.6: Mean excess post-exercise oxygen consumption rate (EPOC) of *Jasus edwardsii* sub-adults at 20°C and 23°C. Horizontal lines represent the pre-exhaustion diurnal routine metabolic rates (Pre-RMR_d) for individuals under absence (solid line; 'Pre-$RMR_{d\text{-}risk}$') and presence of predation risk (dashed line; 'Pre-RMR_{d+risk}'). Asterisks (*) indicate significant differences from a two-tailed independent *t*-test ($p < 0.05$) between pre-exhaustion RMR and EPOC. Vertical bars represent individual variability (mean + 1 SE): – Risk x 20°C (n = 10), + Risk x 20°C (n = 7), - Risk x 23°C (n = 10), + Risk x 23°C (n = 8). Vertical bars represent individual variability (+ SE).

5.6 Discussion

This study examines the influence of projected warmer temperatures on the respiratory physiology of *J. edwardsii* sub-adults under predation risk. Findings demonstrate that at warmer temperatures subadults s altered their metabolic response to perceived predation risk. At the higher temperature (23°C) animals did not reduce their metabolic rate, or display an immobility response, as observed at 20°C. This suggests that at the higher temperatures anticipated under climate change, lobsters might expose themselves to a higher risk of predation. Moreover, elevated energetic maintenance requirements at 23°C suggest that juveniles might need to increase foraging activities, even under the presence of predators, which may impact survival. The following sections first discuss the energetic and ecological implications of higherliving costs for sub-adults living at higher temperatures, and second, examine how the altered anti-predator response may alter key ecological traits such as growth in *J. edwardsii*.

5.6.1 Maintenance energy and aerobic scope

The maintenance requirements, here examined by the standard metabolic rate (SMR), increased exponentially between 14°C and 23°C, as typically observed in ectotherms within their thermal tolerance window (Pörtner 2010). The increasing SMR between ambient (20°C) and warming (23°C) scenarios would suggest that sub-adults will increase their maintenance requirements at projected temperatures for the south-eastern region of Australia. The exponential increase in SMR up to the maximum temperature examined (23°C) suggests that the upper critical temperatures were not exceeded, according to the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis (Pörtner 2010). Previous research on the thermal physiology of *J. edwardsii* would suggest that 23^{o}C would be very close to the critical limits for the species. Using small juveniles (1–5 g), Thomas et al. (2000) reported a decreasing trend in SMR between 22°C and 24°C suggesting that the upper critical temperature limit is within this range.

Aerobic scope (AS) represents the amount of energy available to perform aerobic metabolism above maintenance requirements, a proxy used to assess whole-animal performance and fitness in aquatic organisms (Fry 1947; Pörtner 2010). In this study lobster AS was higher at 20°C than at 23°C, independently of the level of predation risk, suggesting that the upper pejus temperature was exceeded at 23°C. A previous study found that maximum AS of sub-adult *J. edwardsii* was at 13°C (Crear and Forteath 2000) suggesting that both experimental temperatures examined in the present study (i.e. 20 and 23°C) were beyond the upper pejus. Beyond the pejus temperature, overall physiological performance diminishes due to incapacity of the cardiorespiratory system to meet increased oxygen demands associated with elevated metabolism. Nevertheless, further studies examining a broader range of temperatures in juveniles and sub-adults are needed to better define thermal tolerance and associated aerobic performance in *J. edwardsii*.

5.6.2 Routine metabolism under predation risk and temperature

At the ambient temperature scenario (20°C), lobsters exposed to octopus olfactory cues reduced their RMR by 28% during the first hour after KE. The lowering in RMR_{n+risk} would support the immobility response (i.e. move into hiding and reducing activity), which is suggested as an avoidance predator mechanism in *J. edwardsii* (previous chapter). Interestingly, the RMR of lobsters under nocturnal predator risk was similar to the diurnal RMR from controls when lobsters are typically inactive as demonstrated in *J. edwardsii* respirometry experiments (Crear and Forteath 2000). Reduced activity is considered as a taxonomically widespread response to predation risk and an effective mechanism to avoid predation (Sih 1985; Lima and Dill 1990; Toscano and Monaco 2015), commonly reported in aquatic crustaceans such as lobsters (see Hazlett 2011). Alternatively, such immobility response could reflect a reduction in metabolites or chemical cues by lobsters (e.g. 'chemical quiescent') which may minimize predator's perception as discussed in lobsters (e.g. Atema 1995) and other crustaceans (e.g. Díaz and Thiel 2004).

In this study we show that lobster do not display this immobility response at higher water temperatures predicted under a global warming scenario. The lack of such response at 23°C reported

in this study suggests that temperature may inhibit the anti-predator mechanism, increasing exposure and therefore risk of mortality. This may result in a potential trade-off between sheltering and foraging in *J. edwardsii* sub-adults. As animals at warmer temperature have higher energetic requirements in order to support elevated maintenance metabolic costs, increasing activity could be expected in order to cover the required energy intake and would also be associated with increasing foraging rates (Careau et al. 2015). Here, projected temperatures for the region might increase risk-taking behaviour of lobsters due to greater foraging demands and therefore expose lobsters to greater predation risk.

Another plausible explanation of the lack of immobility response at high temperature may be associated with changes in kairomone properties (e.g. protein degradation) as well as kairomone production by octopus under the warming scenario. Recent studies have shown that chemical alarm cues in tropical fish can degrade rather rapidly under natural conditions considering daily changes in water temperature, solar radiation, pH and dissolved oxygen (Chivers et al. 2013). The effect of temperature on the degradation rate of alarm cues may result in seasonal changes in risk perception by prey as suggested by Chivers et al. (2013). It is unclear whether outcomes from our study were affected by the temperature effect on kairomone properties; a consideration that deserves further examination in the current predator-prey model. Alternatively, the lack of immobility response in the warming scenario may have been a result of a low production of octopus kairomone. In our study, octopus individuals were acclimated at the same thermal scenarios as lobsters. Nevertheless, it is unknown whether *P. cordiformis* metabolism was altered under the temperatures tested as the thermal tolerance of this species is unknown. However, under such a hypothesis it is assumed that octopus metabolism is directly linked to kairomone production. Further research is thus needed given the strong relationship between temperature and metabolism in cephalopods (Moltschaniwskyj and Carter 2010).

Routine metabolism during the day (RMR_d) was higher in predator risk exposed animals than in controls at 20°C. This metabolic response could reflect the need to compensate the nocturnal reduction of activity from the immobility response. For example, lobsters might need to compensate

the loss of foraging opportunities during the night by foraging during the day in order to supply enough food to satisfy energetic maintenance costs (Careau et al. 2015). Consequently, the change in foraging patterns may imply a lower risk of predation by octopus with nocturnal predatory habits in rocky reefs (Mills et al. 2008) but a higher predation risk from diurnal predators such as fishes (Mills et al. 2008).

The immobility response of sub-adult lobsters in the present study was more acute (over 1 hour) than in adults (3 hours), although the reduction of RMR was relatively similar (28%) to observations in adult *J. edwardsii* (31.4 %). These differences could be attributable to intrinsic factors such as body size, body condition, sex and age which can affect the way that prey perceive predation risk (Ferrari et al., 2010). For example, large lobsters generally range freely in comparison with juveniles and sub-adults that remain more time within a refuge as reported in *J. edwardsii* (Butler et al. 1999). Social aggregations in juvenile and sub-adult stages are common in spiny lobsters (Childress and Herrnkind 1996; Childress 2007), and especially in *J. edwardsii* (Butler et al. 1999) that seem to be mediated by chemical cues from large conspecifics. This is an important anti-predator strategy in young lobsters although such aggregative behaviour could have a trade-off as high competition for limited dens may occur (Butler et al. 1999) especially in depleted habitats as currently occurring in Tasmanian rocky reefs (Johnson et al. 2011). Additionally, experience also affects how prey individuals respond to predators (Ferrari et al. 2010). For example, predator-experienced individuals are generally more responsive to predator odour compared to predator-naïve individuals (Ferrari et al. 2010). Lobsters used in this study were raised from early benthic stages (pueruli) without any experience of predators (naïve) which could have affected thesub-adults' responses. Alternatively, as juveniles and sub-adults generally have greater mass specific demands, but smaller energy reserves (Jensen et al. 2013; Simon et al. 2015), the risk of starvation could be higher than in adults; clearly, further studies on nutritional condition in sub-adults is warrented.

Individual activity within a respirometric chamber is metabolically expressed as routine metabolism, and studies have defined the relationship between animal behaviour and metabolic rates as a methodological relationship (e.g. Careau et al. 2008). This means that animals that move more in

the chambers consume more oxygen, which has been largely documented in crustacean respiratory physiology (Crear and Forteath 2000; Kemp et al. 2009; Toscano and Monaco 2015). This can be further supported by studies examining circadian patterns in activity and their implications for animal metabolic rates (e.g. previous chapter). In a recent study, Toscano and Monaco (2015) found a mismatch between crab activity within a respirometer and that of crabs in a mesocosm when exposed to waterborne cues from predators. While crabs in a mesocosm showed reduced activity, animals within chambers exhibited greater activity (Toscano and Monaco 2015). As the reduction of activity is widely observed in crustaceans (Hazlett 2011), it has been suggested that increasing oxygen consumption could be due to attempts to hide or escape (i.e. stress) as refuge was not provided within respirometry chambers (Toscano and Monaco 2015). Conversely, the current study did find that lobster subadults decreased their oxygen consumption matching the same behavioural response tested in mesocosms by Toscano and Monaco (2015). The respirometer used here included a shelter inside, probably facilitating the sheltering behaviour of lobsters. Studies testing immobility response should examine methodological differences in order to better determine the linkage between behaviour and physiology.

5.6.3 Escaping responses (tail-flipping) and associated energetic cost

Lobsters did not show differences in AMR at either temperature, independently of the predation risk scenario. Active metabolism (AMR) is associated with maximum short-term energy during forced locomotion (Biro and Stamps 2010), and it is determined in a lobster's respiratory physiology by chasing to elicit tail-flipping (e.g. Jensen et al. 2013; Fitzgibbon et al. 2014). Here, the lobster escape response was similar and was independent of environmental stressors (e.g. warming temperature) and exposure to predator cues. First, the lack of differences in response between temperatures may suggest that subadults reached maximum active metabolism, probably reaching the thermal limits as previously discussed in regard to the aerobic scope. Second, animals did not show differences between predation risk levels, which was expected as tail-flipping is a forced activity. Individual variability was noted between temperatures under predation risk, with larger variability in the ambient

scenario than in the warming scenario. This variability was not examined further in the present study. However, recent studies have demonstrated that metabolic variability can be strongly coupled with behavioural differences of individual animals (Careau et al. 2008).

Sub-adults under both temperatures did not recover to pre-exhaustion routine metabolism levels within the first hour of EPOC, with elevated EPOC under the warming scenario. This suggests a significant anaerobic capacity, such as recently reported in other rock lobster species at similar temperatures (*S. verreauxi*, Fitzgibbon et al. 2014). Such anaerobic capacity is associated with large muscle fibres that facilitate tail-flipping as an escape response (Jimenez et al. 2008). In an ecological context, a predator attack until exhaustion would impose a large energetic cost beside the risk of death.

Recovery periods after exhaustion may take more than 10 hours as recently reported in *S. verreauxi*, demonstrating the large energetic cost associated with tail-flipping in lobsters (Jensen et al. 2013). The EPOC at 20°C and 23°C reported here for sub-adults indicates a considerable energetic cost to restore tissue and cellular homeostasis from exhaustive activity reported in aquatic organisms (Lee et al. 2003). Additionally, preliminary trials in juveniles at 17°C (n = 2) at currently experienced summer temperatures (at facilities where animals were maintained during the course of this study), showed that lobsters were able to recover within the first hour of EPOC (unpublished data). The duration of EPOC increases with temperature in rock lobsters (e.g. *S. verreauxi* pueruli, Fitzgibbon et al. 2014), which may be also the case in *J. edwardsii* sub-adults.

The costs and benefits associated with such a trade-off between growth and predation risk would depend on other extrinsic factors such as habitat conditions, including the shelter-based food supply (Wahle 1992). Although sheltered, sub-adults can increase foraging rates within refuge areas that supply food, allowing a lower exposure to predators compared to larger animals that range freely. Such conditions would be expected to be more limited for lobsters inhabiting low-food habitats, for example *J. edwardsii* inhabiting urchin barrens (Ling 2008). Additionally, structural changes in habitat conditions such as loss of sheltered areas can lead to critical implications for juvenile abundance (e.g. Herrnkind et al. 1997), which can also alter physiology as the lack of shelter can

increase maintenance requirements in aquatic organisms (Millidine et al. 2006; Toscano and Monaco 2015).

Overall, this study demonstrates that temperature can play a crucial role in *J. edwardsii* sub-adults survival, as key anti-predator mechanism such as sheltering might be inhibited by warming temperatures projected for the south-east Australian region. Major findings reported here can serve as an eco-physiological framework for future studies addressing questions regarding predator-prey interactions in this region, particularly potential impacts for the lobster population, associated fisheries and ecosystem functioning.

5.7 Acknowledgements

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5.9 Supporting Information

Table S5.1: Generalized linear mixed models (GLMM) outcomes to test the effect of predation risk (- Risk absence / + Risk' presence) and period (night and day) at 20°C (a) and 23°C (b) on routine metabolicrate.

(a) GLMM - 20° C					
Fixed effect	*Coefficient*	*Std. Error*	*DF*	*t-value*	*p-value*
Intercept	0.08482667	0.009075917	15	9.346347	0.0000
+ Risk	-0.02826417	0.014143795	15	-1.998344	0.0641
Period	-0.01394333	0.004249153	15	-3.281438	<0.01
Period * + Risk	0.01763083	0.006621827	15	2.662533	<0.05
Random effect	*Intercept*	*Residual*			
Std. Dev	0.01929612	0.009501396			
(b) GLMM - 23° C					
Fixed effect	*Coefficient*	*Std. Error*	*DF*	*t-value*	*p-value*
Intercept	0.11811979	0.006194447	18	19.068659	0.0000
+ Risk	-0.00894348	0.009794280	18	-0.913133	0.3732
Period	-0.02086979	0.003165433	18	-6.593030	0.0000
Period * + Risk	0.00575976	0.005004988	18	1.150804	0.2649
Random effect	*Intercept*	*Residual*			
Std. Dev	0.01264338	0.007753695			

Chapter 6:

General discussion and conclusions

The consumptive and non-consumptive effects of octopus depredation have important implications for the southern rock lobster fishery (SRLF), the lobster population and the broader ecosystem. Spatial and temporal patterns in predation risk were evident, as well as influences of lobster size, sex and density. Physiological responses of lobsters to predation risk were marked in adults as well as in sub-adults, suggesting that lobster populations in high-risk areas associated with octopus depredation will likely experience significant non-consumptive effects. Anti-predator responses in sub-adult lobsters were altered under scenarios of increased temperature indicating potential effects of a warming climate on lobster behaviour and possible survival.

There were strong demographic and seasonal components to octopus depredation throughout Tasmania (Chapter 2) and South Australia (Chapter 3). The key factors influencing predation risk in Tasmania were lobster catch rates, fishing effort and temperature. However, eastern and western Tasmanian stock assessment areas exhibited opposing seasonal patterns of in-pot lobster mortality, with high-risk periods being summer and winter respectively. The effect of lobster sex, size and density was evaluated in South Australia showing that in-pot predation risk was elevated with increasing lobster size and was higher for male lobsters which are more catchable by fishing pots in South Australia. Density-dependent in-pot mortality differed across South Australian fishing zones, suggesting an important demographic component to the octopus–SRLF interaction.

Direct consumptive effects are not the only implications of octopus depredation. Using metabolic rates (oxygen consumption) as a proxy of lobster activity, it was evident that *Jasus edwardsii* is able to detect olfactory cues from *Pinnoctopus cordiformis* (Chapter 4). In response to octopus presence, lobsters reduced their metabolic rate suggesting that lobster immobility or sheltering is an important octopus avoidance mechanism. The reduction in metabolic rate occurred at night when lobsters are usually more active, suggesting strong ecological implications as most foraging activity is nocturnal. Animals under predation risk therefore need to trade off or balance the acquisition of food with safety. Such 'decision making' by lobsters is modified by increases in temperature (Chapter 5). Environmental stressors such as warming temperatures could therefore increase the risk of mortality as energetic maintenance requirements, and therefore foraging activity,

are elevated at higher temperatures. Projected increases in temperatures for the south-eastern Australian region are likely to inhibit anti-predator mechanisms in *J. edwardsii*.

Lobster fishing grounds are high-risk environments for lobsters in terms of octopus depredation, having direct effects on the SRLF as well as indirect or trait-mediated effects on lobster populations with potential implications at the ecosystem level.

6.1 Spatial and temporal components of octopus depredation

Annual fluctuations of octopus depredation are an important feature of crustacean fisheries (Garstang 1900; Rees and Lumby 1954; Brock and Ward 2004; Groeneveld et al. 2006). In the SRLF, octopus depredation has strong seasonal and spatial components, differing between major fishing zones as well as within them. Examinations using extrinsic (e.g fishing and environmental factors) and intrinsic (e.g body size, sex ratio and population density) factors of lobster populations were able to provide a 'broad picture' of spatial and seasonal variability of octopus depredation across fishing areas in Tasmania and South Australia. This thesis demonstrates spatially-specific high-risk predation within the north-west and west Tasmanian coasts, at Kangaroo Island, and particularly at the southern fishing zone in South Australia. Additionally, octopus depredation was intensified during the warmer months in northern and western Tasmania, resulting in a positive correlation between lobster catch rates and in-pot lobster mortality. Such spatial and seasonal patterns in octopus depredation could be attributed to local environmental (e.g temperature), oceanographic (e.g up-welling systems) and habitat (e.g bottom type and food availability) conditions that can promote large aggregations of octopus. However, the limited understanding of octopus population dynamics and foraging ecology restricts our ecological framework for interpreting this predator-fishery interaction.

Current knowledge of *P. cordiformis* is based on studies examining population structure and dispersal patterns (Doubleday et al., 2008; Doubleday et al., 2009), as well as reproduction (e.g sexual maturity and fecundity, Grubert and Wadley, 2000) and feeding strategy (Grubert et al., 1999). Unfortunately, these studies are spatially and temporally restricted, limiting a broader understanding

of *P. cordiformis* ecology and biology in lobster fishing areas which were examined in this thesis. By incorporating information on octopus demographic traits such as sex and size, as well as seasonal changes in octopus catch rates by lobster pots, we could achieve a better link between predator and prey at the population level which is desirable to properly assess ecological and economic implications for lobster populations and associated fisheries. In doing so, the examination of environmental and oceanographic conditions in areas where octopus depredation is elevated could inform about octopus population dynamics (Pierce et al., 2005; Robin et al., 2014). Likewise, studies looking at octopus recruitment patterns will be very informative regarding *P. cordiformis* population structure and connectivity as suggested by previous local studies (Doubleday et al., 2009).

Given the spatial and temporal heterogeneity of octopus depredation in the SRLF, outcomes from this study strongly suggest that using an estimate of lobster losses by in-pot mortality that is averaged across time and space (as currently occurs in the stock assessment models) is inappropriate. Although octopus depredation can be relatively modest in terms of total lobster removals, temporal and spatial variability can lead to significant bias for management (Gardner et al. 2011), especially in the context of stock rebuilding (Gardner et al. 2015).

6.2 Lobster demographic traits and octopus depredation

The relationship between lobster catch rates (e.g. survival) and lobster killed catch rate (e.g. mortality) differed throughout the fishing grounds of Tasmania and South Australia, strongly supporting the hypothesis that more than one density-dependent mechanism of octopus depredation exists (Hunter et al. 2005). Depensatory mortality was determined after a consistent inverse relationship between lobster catch rates and lobster killed catch rates was found across Tasmania (Hunter et al. 2005). In this thesis, depensatory mortality occurred throughout the east coast of Tasmania, and was found for the first time in the northern fishing zone of South Australia. However, in-pot lobster mortality appears to be directly related to lobster catches suggesting a strong linkage with high-density lobster areas such as the southern fishing zone in South Australia (McGarvey et al.

1999; Linnane et al. 2008). These two relationships may reflect type I (direct response) and type II (an inverse response) predatory responses (see Holling 1959; Hunsicker et al. 2011), although further studies exploring important behavioural predator traits (e.g. handling time, Holling 1959) are required to confirm such assumptions.

This thesis provides new insights regarding sex- and size-related mortality by depredation, particularly once lobster catch rates were included (e.g. density-related mortality). Large males were more likely to be killed by octopus, a pattern consistent across fishing zones and extending previous observations in South Australia (Brock and Ward 2004). Size- and sex-dependent lobster mortalities by octopus appeared to mirror lobster catchability in this fishery as large males are more dominant in lobster pots (Frusher and Hoenig 2001; Ziegler et al. 2004). This leads to questions regarding selective predatory behaviour by octopus (e.g. targeting the largest individuals) as opportunistic behaviour (e.g. killing what is available) is generally assumed (Robin et al. 2014).

6.3 Potting and its implications for the magnitude of octopus depredation

Fishing effort had a major influence on octopus depredation throughout the east coast of Tasmania, especially during the winter fishing season when fishers deploy more lobster pots. Depensatory mortality was observed during winter fishing on the east coast, suggesting that the seasonality of water temperature may not be modulating octopus depredation on this coast as conversely observed on the west. Although further studies are needed to elucidate the role of fishing effort on octopus depredation, these findings suggest that fishing can attract octopus onto fishing grounds seasonally (e.g. summer-high in-pot risk), as well as facilitating acquisition of food during cold periods when lobster catches are low (e.g. winter-high in-pot predation risk). *Pinnoctopus cordiformis* seems to show a vertical migration during late spring (Anderson 1999), with high occurrence of octopus caught by the SRLF during summer (October–March) (Linnane et al. 2014a,b). This leads to important questions regarding octopus foraging ecology in areas where lobster fishing is high, and potential impacts on octopus migration patterns that may be strongly modulated by

energetic demands associated with growth and reproduction (Robin et al. 2014). It is therefore expected that octopus feeding behaviour upon lobster catches may differ among sex, especially if the octopus breeding season implies a strong reduction in food consumption by females during spawning (Boyle and Rodhouse, 2005; Robin et al. 2014). Understanding the relevance of key octopus intrinsic characteristics such as sex and body size on the patterns of depredation would be able for exploring these relationships further.

As suggested in the depredation of cetaceans within long-line fisheries (Hamer et al. 2012), the SRLF is likely to reduce the energetic costs of octopus foraging upon caught lobsters in comparison with free lobsters which are very successful in escaping from octopus attacks in open areas (Bouwma and Herrnkind 2009; Buscaino et al. 2011). Recent studies have suggested that lobster fisheries can act as a subsidy food supply on the fishing grounds (e.g. Waddington and Meeuwig 2009), attracting predators such as octopus (Phillips et al. 2012) and sharks as reported in the SRLF in Tasmania (Barnett et al. 2013). The spatial and seasonal characterization described here for Tasmanian and South Australian fisheries supports the hypothesis that the lobster fishery plays an important role in modulating the frequency and magnitude of octopus depredation. The examination of octopus habituation to lobster fishing gear is crucial, as reported in other predator-lobster fishery interactions in Tasmania (e.g sharks, Barnett et al. 2013), which is an important step towards an enhanced understanding of octopus depredation. For example, a proper quantification of lobsters and bait consumed by octopus from stomach contents could inform about the level of habituation of *P. cordiformis* on the SRLF. Future studies should also examine key behavioural components such as frequency of octopus depredation at daily scale, as well as the handling time by octopus inside pots and its relationship with lobster catches. The later will allow a better definition of predatory responses (Holling, 1959) as hypothesized from this thesis (Chapter 3). Additionally, contrasting such information with octopus consumption upon free lobsters may inform about the octopus learning process under different potting scenarios as suggested earlier. All these questions reinforce the need for further research on octopus ecology and population dynamics and its implications for lobster populations and associated fisheries.

If we consider that an octopus can enter traps, feed (~3 hours, Brock et al., 2003) and escape before the lobster pots are hauled in less than 24 hours (Groeneveld et al., 2006), then the impact of octopus depredation could be partially proportional to the soak time. Previous studies on octopus depredation (Brock and Ward, 2004; Groeneveld et al. 2006) have demonstrated a direct effect of soak time on in-pot lobster mortality resulting in an elevated depredation level with a longer soak time (e.g > 24h). This has been preliminary supported by studies examining double night fishing effort (soak time of 9.5 hours), and its effects on in-pot lobster mortality, resulting in a lower in-pot predation risk than standard shots (12. 5 hours) in Tasmania (Green et al., 2009). Additionally, the frequency of the interaction appears as a key component to quantify the magnitude of octopus depredation.This could be important to examine throughout the fishing season as within-season changes of octopus caught by the SRLF may occur (Harrington et al. 2006). Future studies examining the effect of soak time, including spatial variability, will contribution to enhancing our understanding of octopus depredation. Using direct observations (e.g video camera studies) could provide insights into when octopus enter traps (randomly or mainly after lobsters have entered), indicate the behaviour of both lobster and octopus in traps including prey handling times and any selective behaviour (e.g targeting of large lobsters).

Lobsters and octopuses generally seek the same habitat type (e.g. crevices), and sometimes they can consume similar prey items such as molluscs. Hence, octopus can affect lobster survival (via predation), but can also affect habitat use in lobsters as a result of competition for shelters and food (Berger and Butler 2001; Butler and Lear 2009). Overall, lobsters will avoid cohabitation with octopus as reported for *J. edwardsii* (Anderson 1997). I hypothesise that octopus depredation might also cause changes in lobster foraging rates and habitat use as reported for other species under predation risk (Childress and Jury 2006). This thesis provides key mechanistic information to support such a hypothesis as lobster physiological responses under predation risk were found.

6.4 Physiological responses under predation risk – defining anti-predator mechanisms

Generally, lobsters increase their oxygen consumption during the night as they become more active in contrast to day time when they are less active. This clearly demonstrates that *J. edwardsii* experiences higher energetic costs during the night, especially during foraging activities as demonstrated in the field (MacDiarmid et al. 1991) and captivity (Oliver et al. 2006). Such clear diurnal changes in lobster routine metabolic rates allowed the establishment of energetic demands associated with lobster activity in the ecological context of predation risk.

Significant changes in lobster metabolic rates occurred when individuals were exposed to octopus olfactory cues at night. *Jasus edwardsii* adults strongly reduced their oxygen consumption immediately after exposure to octopus cues, returning to pre-exposure levels in around five hours. Such a metabolic response under predation risk by lobsters is hypothesized to reflect a reduction in lobster activity (i.e immobility), a suggestion strongly supported by previous studies on crustaceans (Hazlett 2011). Briefly, the immobility response is here used as a proxy of sheltering behaviour which generally observed either in lab or field conditions when lobsters are exposed by chemical cues from predators (see Hazlett, 2011). Lobsters can also attempt to escape when experiencing predation attempts from octopus ('tail-flipping', Buscaino et al. 2011), however, this incurs high energetic costs for individuals (Jensen et al. 2013) in comparison with sheltering. Although both anti-predator responses are effective at reducing the risk of octopus predation, increasing sheltering behaviours during the night might result in negative effects on lobster growth as foraging rates would be reduced, as broadly reported for other taxa (see Hawlena and Schmitz 2010). Alternatively, other physiological mechanisms may be used, such as reducing chemical cue emissions to remain 'chemically quiet'. This has been demonstrated in the context of mating (Atema, 1995; Diaz and Thiel, 2004), but has unfortunately this 'chemical quiescence' hypothesis has not been contextualized into a predator-prey context. This deserves attention from future studies.

Environmental stressors such as increasing water temperatures will increase metabolic rates and require increased food intake and thus heighten the risk to lobster predation through increased foraging. Using *J. edwardsii* sub-adults to examine vulnerability in a climatic context, this thesis

contributes new insights about the thermal physiology of this species and how this intersects with predator–prey interactions. Forecasted thermal scenarios (e.g. 23°C) for the south-east coast of Australia under climate change (e.g. 2060 yr under A1F1 scenario, IPCC 2007) increased the energetic costs of maintenance requirements. Individuals reduced their oxygen consumption by 23% at the ambient scenario (20°C) in comparison with controls when exposed to octopus cues, validating previous findings (e.g. immobility response). Conversely, lobsters maintained at 23°C showed the same pattern in oxygen consumption when exposed to predator cues, suggesting that increased temperatures can override the anti-predator responses of sub-adults in this species. Similar to recent studies in marine predator–prey systems (Matassa and Trussel 2014b), outcomes from this study may serve as a base line for future studies examining trade-offs between growth and sheltering under projected environmental conditions for the region, with important ecological and economic consequences for the ecosystem and the *J. edwardsii* fishery.

6.5 Uncertainties and the need for an integrative approach

Empirical studies have consistently demonstrated that prey individuals must balance the demand for food with the need for safety under predation risk (i.e. prey decision making, Sih 1985; 1992; Lima and Dill 1990). Individuals under predation risk increase their sheltering behaviour to maximize survival, although the subsequent reduction in foraging activities profoundly impacts growth and reproduction (i.e. the growth/predation risk trade-off, Lima and Dill 1990). The growth/predation risk trade-off is used here as an ecological and ecosystem framework, to discuss the outcomes of this thesis, in addition to recent information on indirect trait-mediated effects of predators (Werner and Peacor 2003) in marine communities (Trussell et al. 2006; Long and Hay 2012; Matassa and Trussell 2014a, b). Using this perspective, this thesis provides the basis for discussions and new ideas regarding the implications of octopus depredation on lobster populations and their associated fisheries and ecosystems, and could provide a strong basis for investigations and developing an understanding of key processes and impacts in other fisheries where depredation occurs.

6.5.1 Population implications

Outcomes from physiological studies were able to provide mechanistic information regarding anti-predator responses which may serve as a first step to examine changes in lobster activity (e.g foraging vs sheltering) under predation risk. Recent studies have demonstrated that predator identity can modify the strength of anti-predator responses in juvenile lobsters (*H. americanus*, Wilkinson et al., 2015). Furthermore, field studies using telemetry were able to demonstrate that lobsters exposed to predator presence can reduce their maximum daily home range area and decrease the distance they travelled from their shelter area (McMahan et al., 2013), suggesting important implications for growth performance and associated impacts at the lobster population level as reported in NCE's in marine communities (Matassa and Trussell 2014 a,b). Unfortunately any understanding of NCEs in *J. edwardsii* population is completely absent, and deserves attention in future studies.

A hypothetical model examining the implications of an expansion or contraction of home range under octopus absence or presence on the fishing grounds is presented (Figure 6.1). The presence of octopus is likely to increase sheltering behaviour and is expected to reduce lobster catchability for the fishery. Briefly, the probability that a lobster will enter a trap and be captured is likely dependent on the area of bait influence (ABI). The ABI is defined as "the area within which the bait can be detected where it exerts a measurable influence on orientation and movement of the target species" (Bell et al. 2001). It is unclear whether a predator's presence may modify the ABI especially in areas under high in-pot predation risk, either by octopus proximity perceived through kairomones or by alarm cues from killed or damaged conspecifics (see Shabani et al., 2008) inside fishing gear. The concentration of octopus kairomone required to trigger lobster anti-predator responses such as immobility is unresolved, demonstrating the need for future studies integrating lobster chemical ecology into a fishing context.

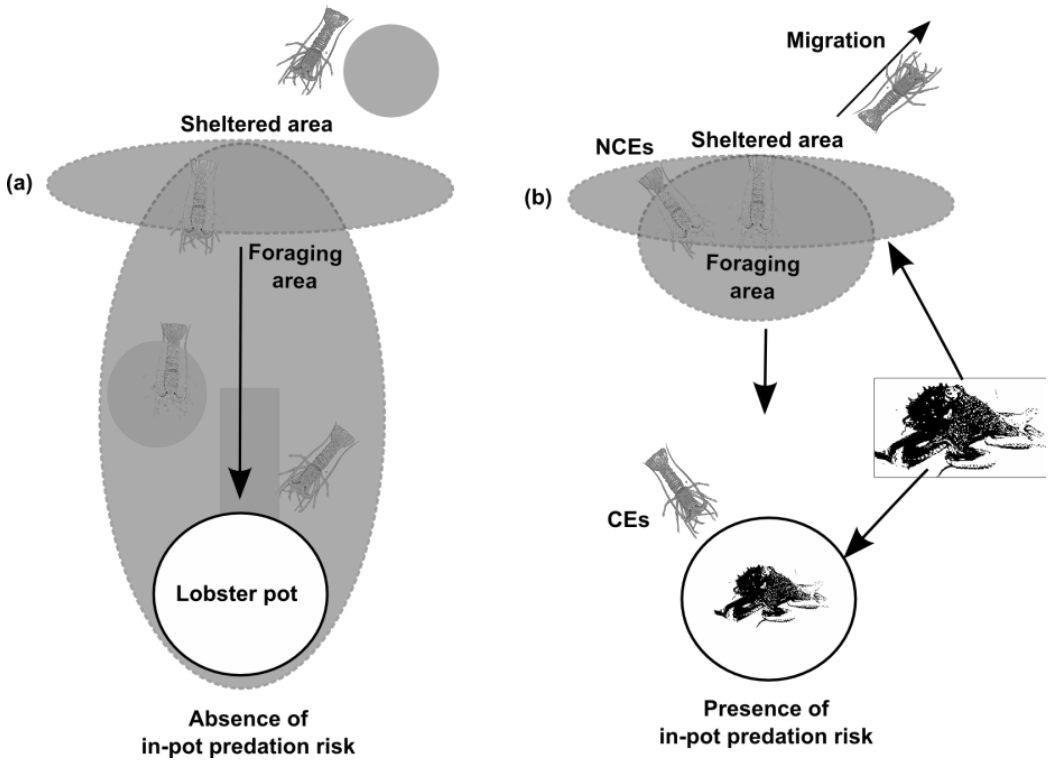

Figure 6.1: A conceptual model suggesting changes in *Jasus edwardsii* – fishery interaction by consumptive (CEs) and non-consumptive (NCEs) effects of octopus (*Pinnoctopus cordiformis*) depredation. In-pot lobster mortality causes direct impacts on lobster population by density-dependent mechanisms, with an increasing risk for large and male lobsters. However, octopus depredation might also cause competition by habitat given similar habitat preferences by octopus. Here, NCEs might occur as octopus presence will force decision making (e.g. food vs safety) by lobsters, therefore potentially restricting the foraging area which may impact lobster catchability. This could also cause lobster to move away from areas at high-predation risk with uncertainties for lobster population and the fishery.

Prey individuals under predation risk can undergo to a 'risk-reckless' response when starving risk increases as shown in previous lobster studies (Spanier et al. 1998). Nevertheless, such increase in foraging rates can lead to less selectivity by lobsters when choosing prey items, and ultimately, consuming fewer calories than lobsters foraging in the absence of predators (Spanier et al. 1998). Importantly, such a sub-optimal feeding strategy may reduce the moult increment and lengthen the intermoult period (Waddy et al. 1995). Here, such a risk-reckless response could be even more dramatic for individuals entering into the moulting cycle as they need a reserve accumulation period to fuel the growth process. After moulting, lobsters steadily increase their feeding rates to cope with larger energetic demands (Simons et al. 2015), reflecting important seasonal changes in lobster catchability by the SRLF (Ziegler et al. 2004). The NCEs from octopus depredation towards the

lobster population could therefore be magnified if it occurs during the period of accumulating energetic reserves. It would be of interest to understand how the amount of foraging time 'lost' by octopus depredation can impact lobster growth performance, and this should be properly examined by future investigations looking at NCEs in *J. edwardsii* populations.

Lobster fisheries are well known to skew the sex ratio towards females, reducing the size advantage of reproductive males (MacDiarmid and Saint-Marie, 2006) which may lead to alterations in sexual competition, sexual conflict and mating (MacDiarmid and Saint-Marie, 2006). Monthly variation in lobster catch rates (examined here by random effects mixed modelling) suggest that size-, sex- and density-dependent lobster mortality via octopus depredation might vary strongly throughout the fishing season, following seasonal changes in lobster catchability (Ziegler et al. 2004). Such seasonal changes, in addition, can result in important changes in size and sex dominance within lobster pots (Frusher and Hoenig 2001; Ihde et al. 2006). It is possible that octopus depredation could exacerbate fishery impacts on lobster populations throughout the fishing season as depredating octopus will remove what is more available from the trap, including large males as well as ovigerous females. Future modelling studies could examine how octopus depredation may impact key lobster reproductive traits (e.g egg production) at seasonal and spatial scales by integrating lobster killed size and sex probability into current lobster biomass projections models. Outcomes from such modelling approaches will result in valuable information for fishing areas impacted by high predation risk, allowing a better understanding of economic and ecological impacts related to octopus depredation.

6.5.2 Ecosystem implications

Theoretical and empirical works have stated that mid-trophic predators are more prone to being affected by NCEs (Trussell et al. 2006), especially those species inhabiting resource-rich systems (McNamara and Houston 1987). As food-rich habitats promote good nutritional status for prey, individuals experiencing predation risk can cope better with NCEs (e.g. sheltering for a prolonged period of time) reducing the risk of starvation. In addition, predation risk can lead to important

changes in ecosystem functioning and structure by diverting energy and nutrients away from growth, altering nutrient cycling and energy efficiency across trophic levels (Trussell et al. 2006; Hawlena and Schmitz 2010).

On Tasmanian rocky reefs, *J. edwardsii* is a mid-trophic predator consuming ascidians, urchins and gastropods (Guest et al. 2009). Importantly, this species plays an important ecosystem role by controlling overgrazing urchin populations along eastern Tasmania (Ling 2008; Johnson et al. 2011). However, fishing has been suggested to limit the controlling capacity of lobsters as fishers remove larger lobsters from the population and it is large lobsters that prey on the urchins (Ling et al. 2009a,b). As reported in this thesis, size-dependent lobster mortality by octopus depredation can exacerbate removal impact on large lobsters by the fishery. Future studies examining ecosystem uncertainties in areas experiencing high-predation risk are highly recommended. Such a lack of understanding was recently highlighted by modelling studies on marine communities under climate change in south-eastern Australia (Marzloff et al. 2016).

Animals have successfully evolved to maximize survival when predation risk is elevated (Lima and Bednekoff 1999), but such conditions could be complicated for young lobsters given their high dependencies on shelters (e.g. food-based shelters, Wahle 1992). Hence, the strength of NCEs on lobster populations may be strongly associated with lobster size, and changes in habitat conditions (e.g. kelp forest vs urchin barrens) may increase such NCEs. For example, local investigations suggest that the structural complexity of the kelp forest may reduce the risk of predation in early benthic stages of *J. edwardsii* in comparison with low-quality habitats (Hinojosa et al. 2014). Likewise, food supply for lobsters in terms of abundance and diversity of items could also be restricted in urchin barrens (Ling 2008).

Water temperature can modulate the strength of NCEs in marine communities (e.g. Matassa and Trussell 2014a) as reported in the current study with sub-adults, with critical implications given future environmental changes in the south-east Australian region (Pecl et al. 2009). The increase intake-model (Careau et al. 2015) suggests that juveniles will increase their foraging rates to supply enough energy for elevated living costs. It has been demonstrated that animals living in food-rich

conditions can cope much better with predation risk as they are able to build energetic reserves used during sheltering (Matassa and Trussell 2014b). It is unclear how warming temperature and the reduction of habitat quality via, for example, urchin barrens can modulate the strength of NCEs on lobsters in this fast-changing region (Johnson et al. 2011; Marzloff et al 2016). In addition, the lack of information on how chemical cue properties (e.g degradation rate, Chivers et al. 2013) can be altered under environmental variability requires future studies. At the same time, the environmental-mediated metabolism of octopus would suggest that kairomone emission by octopus may also be altered under warmer temperatures. Such a scenario should be properly investigated to elucidate how chemically-mediated predator-prey interactions will play out in a climatic context.

The potential for *P. cordiformis* to alter its trophic ecology on the lobster grounds is a question that deserves more attention, particularly given the existence of predator habituation in the SRLF (Barnett et al. 2013). Uncertainties regarding the trophic role of octopus on the fishing grounds limit a more complete understanding of the ecosystem implications of octopus depredation, although several local studies have reported *P. cordiformis* in the diet of top predators (Imber 1999; Hume et al. 2004; Lalas 2009; Pethybridge et al. 2011; Barnett et al. 2013). The interaction between octopus and its predators within lobster pots warrants more investigation, especially if sharks caught by the SRLF generally consume *P. cordiformis* and *J. edwardsii* (Barnett et al. 2013). Species interactions within lobster pots are complex, and further studies should consider in-situ observations in order to better define the frequency and magnitude of depredation in the SRLF.

Recent studies have highlighted the need to develop physiological proxies considering multiple factors (Zanette et al. 2014). This is a suitable challenge for future research aiming to define physiological responses of lobsters under predation risk. A recent investigation undertaken in Tasmania has provided key information on the health, physiological and nutritional status of *J. edwardsii* on the fishing grounds (Simon et al. 2015), and these methods may be applicable to determining physiological stress in lobster populations inhabiting high levels of predation risk. New disciplines integrating eco-physiological traits of aquatic organisms into management and conservations decision-making are quickly emerging (Cooke et al. 2013). Physiological

characterizations of lobster populations are very useful in an ecosystem context, and demographic traits (e.g. abundance and distribution) can be defined from key physiological mechanisms (e.g. thermal tolerance and aerobic scope), enhancing our knowledge for managing human impacts on natural resources.

A summary of key findings as well as uncertainties at population and ecosystem levels discussed in this section is provided in Figure 6.2.

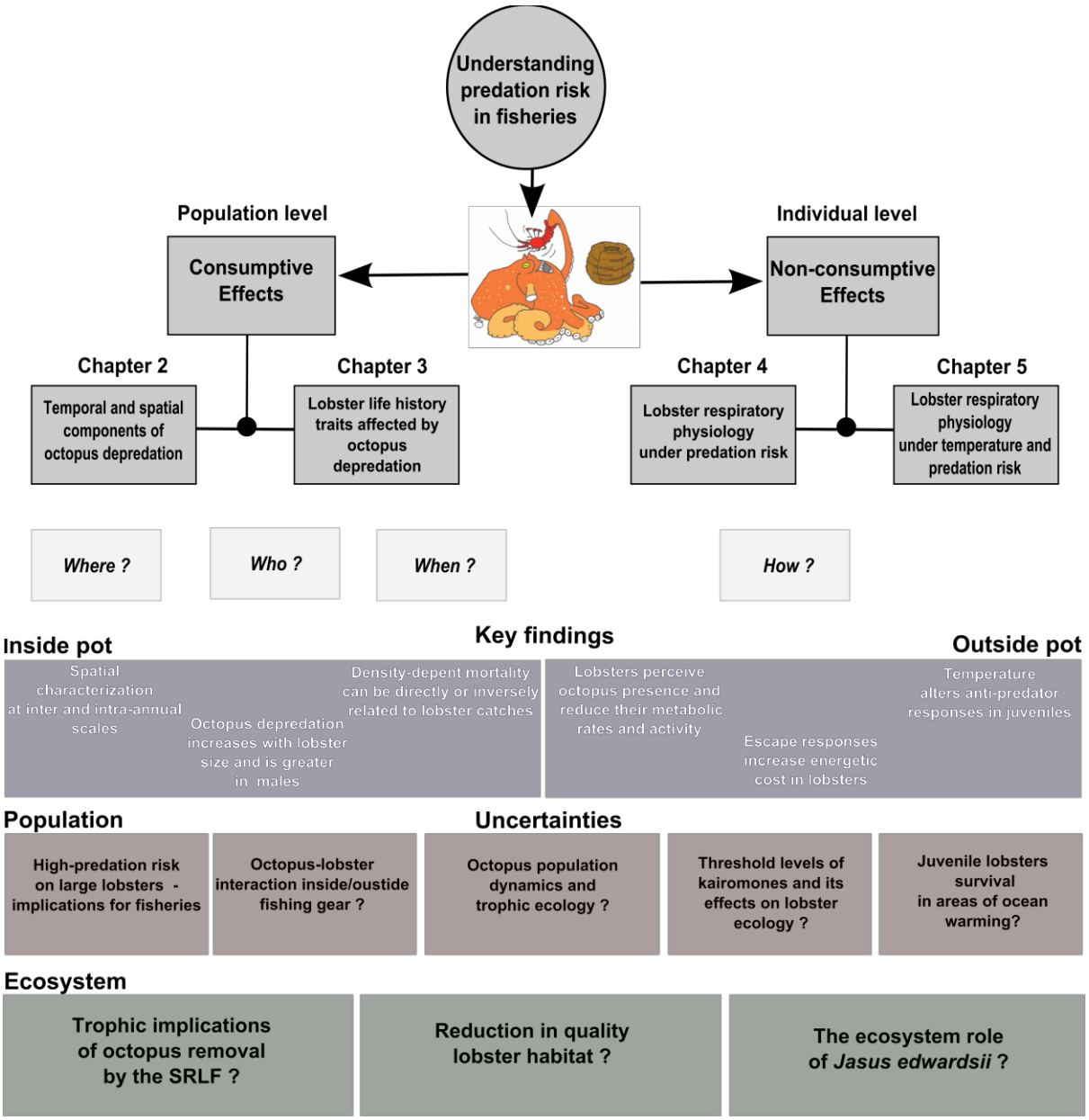

Figure 6.2: Structure and key findings from this thesis, with uncertainties at population and ecosystem levels.

6.6 Conclusions

Understanding predator–prey interactions in marine fisheries is crucial for development and implementation of ecosystem-based management approaches (Pikitch et al. 2004; Francis et al. 2007). This thesis represents a first attempt to provide an eco-physiological framework to examine the process of octopus depredation within the southern rock lobster fishery in Australia from the perspective of individuals, populations and the fishery. Currently, octopus depredation is considered as a steady-state process for fishery management, resulting in important biases as this source of lobster mortality is a highly spatially and temporally variable and dynamic process as demonstrated extensively in this thesis. A suitable characterization of in-pot lobster mortality is now available for major fishing areas and throughout the fishing season in Tasmania and South Australia, allowing a better definition of ecological and economic implications from octopus depredation for lobster populations and the associated fisheries. However, information on octopus population dynamics and foraging ecology is urgently needed to achieve a broader ecological perspective of this predator-prey-fishery system. Outcomes from this study strongly suggest that the fishing can substantially modulate the frequency and magnitude of octopus depredation, which is likely to act as an important source of food for octopus populations inhabiting fishing grounds. This leads to important questions regarding octopus habituation to lobster fishing gear, and in particular how such an octopus feeding strategy can impose trait-mediated effects on lobster populations by altering key ecological functions such as foraging.

Octopus presence can modify key Jasus edwardsii traits such as metabolic rates via chemical signalling (e.g predator cues or kairomones). A reduction in lobster metabolic rates suggests that the immobility response may maximize lobster survival, although this then creates challenges for ing individuals to compensate energetic demands. This is particularly the case under scenarios of warming waters as explored here. This leads to important questions into a fishing context as changes in lobster foraging rates may impact catchability. For lobster grounds under high predation risk, this would be particularly important to understand. Future research in these areas would be is pivotal to

enhance the current energetic approach explored here, especially to scale-up how changes in lobster foraging ecology may impact lobster population and fisheries, as well as ecosystem functioning and structure.

A thorough understanding of predator–prey interactions requires integration of consumptive (Hurrisken et al. 2010) and non-consumptive (or indirect trait-mediated effects, Werner and Peacor 2003) mechanisms and the consideration of physiology, ecology and fisheries (i.e. conservation physiology, Cooke et al. 2013). This study provides a comprehensive baseline for future studies to examine in detail some of the complexities and key questions identified throughout the thesis. For example, trait-mediated trophic cascades can rise as a result of in-pot predator–prey interactions, influencing the structure and function of ecosystems and the implications that this may have on the productivity of fished resources.

6.7 References

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